A REVIEW OF BRACHIOPOD DOMINATED PALAEOCOMMUNITIES FROM THE TYPE ORDOVICIAN

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ABSTRACT. Recent studies on Ordovician (mainly Llanvirn to Caradoc) faunas from type and classical localities in Wales and the Welsh Borderland have resulted in the publication of a wealth of data representing approximately 200,000 individual identifications from about 2,000 samples (assemblages) collected through some 10 km of strata (average sample interval 5 m). Contributing authors have named at least thirty variously defined assemblages, associations, sets, communities, and palaeocommunities which are reviewed and subjected to cluster analysis. This reveals eight highly correlated ($p > 95\%$) taxonomic subclusters which also closely reflect palaeogeography, stratigraphic relationships, and facies preferences. These are conveniently characterized, using pre-existing guidelines, as the 'mixed' *Dalmanella*, *Hesperorthis*, *Lingulella*, *Onniella*, *Dalmanella*, *Bancroftina-Kjaerina*, *Howellites*, and *Nicolella* palaeocommunities. Other important faunas include inarticulate brachiopod associations dominated by *Monobolina*, *Pseudolingula*, and *Schizocrania*.

Palaeoecological and evolutionary considerations indicate a marked contrast between widespread and diverse, biologically accommodated associations from the middle part of the facies (textural) spectrum and localized, physically limited, low-diversity faunas from extremely coarse (shoreface) facies and more widespread low-diversity faunas from very fine (offshore) facies. This pattern differs from some Silurian models but accords with others. Differences in the Welsh Basin during the two periods suggest that comparisons between supposedly analagous palaeocommunities are tenuous and certainly not viable from a taxonomic viewpoint. Diversity, facies preference, palaeogeography, and taxonomic composition are all shown to be useful guides to palaeocommunity evolution; they indicate that high-diversity, pre-Caradoc, *Dalmanella*-dominated faunas represented the most stable palaeocommunity which evolved in basinal (open-shelf?) rather than basin-margin (shoreface) localities to give rise to associations characterizing the *Nicolella* palaeocommunity of Caradoc times. In contrast, low-diversity shoreface faunas show more rapid and unpredictable change whilst those from argillaceous offshore facies remain unchanged over long periods.

THE aim of this paper is to summarize the results of a long-term, integrated research project on the Ordovician (Llanvirn to Caradoc) shelly facies of the Anglo-Welsh region and to assess the importance of named palaeocommunities and their role in community evolution. The studies on which this review is based were virtually all inspired by Dr. Alwyn Williams, who together with the author and Dr. J. M. Hurst has been largely responsible for the completion of the main quantitative taxonomic and palaeoecological contributions listed in Table 1.

Other important studies by Drs. P. J. Brenchley and R. K. Pickerill, although more localized and involving different methodology, contribute to our knowledge of contemporary ichnofaunas and to the growing pool of interpretative ideas. Indeed, the spate of recent publications (Table 1) has resulted in such an accumulation of data and contrasting ideas on the factors responsible for controlling the distribution of Ordovician faunas that it seems particularly advisable to rationalize and compare contrasting opinions and sometimes ambiguous terminology before proceeding further.

Viewed in the historical context of British Lower Palaeozoic palaeoecological research, the community concept was applied later to Ordovician faunas than to those of the Silurian (e.g. Ziegler 1965) and can consequently be considered more thoroughly in the light of the substantial quantitative research which has been completed in the last decade. To date over fifty distinct faunal associations and communities or palaeocommunities have been named and defined quantitatively. The documented taxonomic composition of these and other representative assemblages (data in

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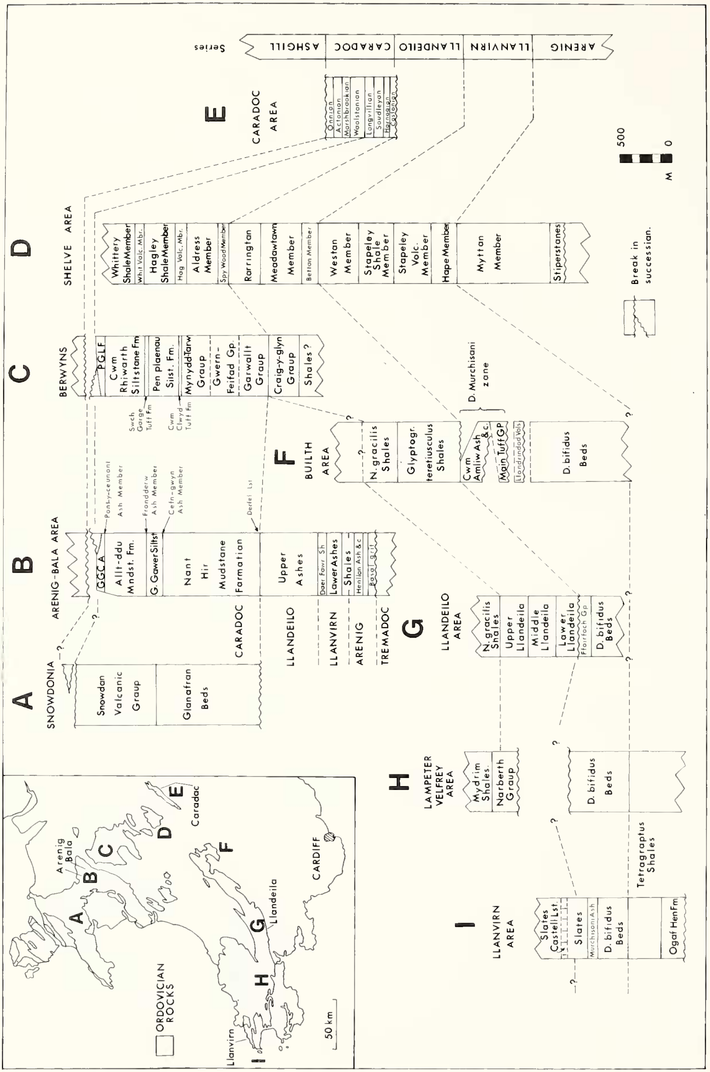


TEXT-FIG. 1. Correlation of type and classical sections in the Ordovician of Wales and the Welsh Borderland.

Table 5) affords the opportunity for a comprehensive cluster analysis which is used as a guideline for delineating major palaeocommunity patterns.

This review deals specifically with Anglo-Welsh faunas, which belong to an entirely different Ordovician province than those of Scoto-Irish or Scoto-American affinity (Williams 1962). Although brief observations on Anglo-Welsh Arenig faunas are relevant to discussion of descendant associations, and those of 'Ashgill' age often resemble ancestral Caradoc faunas, detailed discussion of the faunas of these series is largely outside the scope of this study.

This analysis critically examines known associations, and is broadly divided into two parts. Initial sections attempt to rationalize definitions and ambiguities or inconsistencies in documentation and, like the necessary discussion of local faunas, may be of greater interest to the more specialized reader. The latter part of the paper encompasses more generalized conclusions and outlines the eight major palaeocommunity groupings listed in the abstract (I–VIII of text-fig. 10). These can be shown to have been associated with particular sedimentary deposits located along a facies gradient inferred to represent a generalized shoreface to offshore transect. The model is substantiated by diversity profiles which are analogous to modern and fossil examples for similar transects. Palaeogeographical, palaeoecological, and taxonomic considerations shed light on probable patterns of community evolution.

TABLE 1. Summary of studies relating to Anglo-Welsh, Llanvirn to Caradoc Brachiopoda and palaeoecology (1973–1980); standard sections for key areas shown in text-fig. 1. (*NS* = number of samples; *M* = approximate thickness of strata [metres]; statistics (right) summarized in abstract.)

Area	*Age of faunas*	*Author*	*NS*	kg	*M*
Shropshire	Upper Caradoc	Hurst (1978*a*, *b*; 1979*a*, *b*, *c*) Hurst and Hewitt (1977) Hurst and Watkins (1981) Harper (1978)	260	(2000)	300
	(Lower Caradoc	Hurst and Lockley in prep.)	179	—	300
Shropshire	Arenig–Lower Caradoc	Williams (1974, 1976)	222	—	4500
Bala, Gwynedd, N. Wales	Lower Caradoc	Lockley (1977, 1978, 1980*a*, *b*)	250	1500	1500
Berwyn Hills, Powys Clwyd, N. Wales	Lower Caradoc	Brenchley (1964, 1966, 1969, 1972, 1979) Brenchley and Pickerill (1973, 1980) Pickerill (1973, 1974, 1975, 1976, 1977) Pickerill and Brenchley (1975, 1979)	400+		2000
Llandeilo, Dyfed	Llandeilo	Wilcox (1979) Wilcox and Lockley (1981)	395	1400	1100
Dyfed	Upper Llanvirn–Lower Caradoc	Addison (1974) Lockley (this paper)	80		
Llandeilo and Builth	Upper Llanvirn–Llandeilo	Williams, Lockley and Hurst (1981) Lockley and Antia (1980) Lockley and Williams (1981)	120	800	100+
South-west England	?Llandeilo	Cocks and Lockley (1981) Bassett (1982)			

PALAEOECOLOGICAL DEFINITIONS AND CONCEPTS

Since Williams (1973, p. 242) summarized the implications of his investigations into the Lower Caradoc brachiopod faunas of North Wales (Williams 1963) by suggesting that the *Dinorthis*, *Nicolella*, *Onniella*, and *Howellites* 'associations dominated the brachiopod communities of those times', a considerable volume of mainly quantitative palaeoecological research has been directed towards further investigation of these and related ancestral 'associations'.

It is therefore desirable to provide an unequivocal explanation of the concepts and criteria employed in grouping fossil remains into categories like assemblage, association, or community. Definitions proposed by Pickerill and Brenchley (1975; 1979, p. 237) furnish useful guidelines worth quoting:

> (i) An assemblage refers to a single sample.
> (ii) An association refers to the recurrent association of taxa in a group of assemblages.
> (iii) A community refers to a spatially and temporally recurring group of organisms usually related to specific environmental parameters.

Such a hierarchical arrangement is generally acceptable and at least partially conforms with the terminology applied by other authors. However, ambiguities arise from the finely drawn distinction between the terms 'association' and 'community' and the fact that several authors (e.g. Williams 1976; Hurst 1979*b*; Lockley 1980*a*) have tended to avoid using the latter category because of its inherent biological implications. Indeed Williams (1976) even preferred the 'non-committal' mathematical label 'sets' for groupings defined by cluster analysis, although this term has also been misinterpreted (Raab 1980). Similarly, Williams *et al.* (1981) grouped related 'associations' into 'palaeocommunities', so as to emphasize the residual nature of all fossil faunas.

Although well rationalized, the definitions of Pickerill and Brenchley (1975, 1979) indicate the difficulty of drawing clear distinctions between the terms 'association' and 'community', which are both based on recurrent patterns in constituent taxa. Although they contend that communities are related to environmental parameters, Williams (1973) had already stated that his associations were facies-related. These authors therefore provide examples of the largely synonymous use of the terms 'association' and 'community'; e.g. after considering entire assemblages Pickerill (1974, 1975, 1977) and Pickerill and Brenchley (1979, p. 230) 'adopted' the named associations of Williams (1973) and elevated them to community rank. They also referred to subcommunities 'to distinguish associations within a community which have a different abundance of constituent genera', thereby introducing a new category which barely differs from the other two. Such hazy terminology is undesirable but hard to circumvent; the term 'association' is particularly ambiguous and can apparently be endowed with increasing degrees of 'biological' emphasis until it becomes a 'community' (cf. Pickerill and Brenchley 1979). This may be acceptable where an association of similarly composed recurrent assemblages can be shown to represent an *in situ* residuum of a biological community, but is obviously unacceptable where there is evidence of continued reworking or persistent physical environmental controls.

Where a locally defined association reappears after a temporary displacement it is best referred to as a subsequent 'phase' (*sensu* Hurst 1975, 1979*b*; Lockley 1980*a*; Williams *et al.* 1981); these can be numbered sequentially. The term faunule, used for collective reference to both formally and informally defined associations, phases, and assemblages (Wilcox and Lockley 1981), is too generalized for formal definition and is used only for convenience.

Such rationalizations lead to the following summary of categories for fossil residua:

1. An 'assemblage' refers to a single sample from a particular horizon. It may be transported, partially 'disturbed' (*sensu* Scott 1974) or an *in situ* residue; it can be analysed conveniently using individual 'census samples' (cf. Williams *et al.* 1981).
2. An 'association' refers to a group of assemblages all showing similar, recurrent patterns of species composition; its origin, like that of its component assemblages, may vary from one association to the next.

(3) A palaeocommunity (or fossil community) refers to an assemblage, association, or group of associations and/or phases of associations inferred to represent a once distinctive biological entity. The term palaeocommunity helps draw a useful distinction between the small preserved part of a biological community and the more complete entity which may be inferred or represented in exceptional cases. The term is used here only to categorize associations which are closely related in terms of taxonomic composition, palaeogeography, age, and facies preferences. (This definition also accords with that proposed by Kauffman and Scott (1976).)

Having defined an association or paleocommunity, various criteria may be employed in choosing an appropriate name. Fortunately, in the context of British Ordovician research all workers have consistently chosen to name associations and communities after dominant (relatively abundant) constituents. Less dominant species may be chosen and justified on the basis of distributions considered to be ecologically significant when using such parameters as fidelity or exclusiveness (see Krebs 1978 for definitions). However, the naming of communities after rare taxa (e.g. Titus and Cameron 1976) often obscures similarities which might otherwise be immediately apparent (cf. Lockley 1980*a*, pp. 192, 229).

Proportions of residual fossil species within an undisturbed association or community may be considered analogous to proportions found in populations in modern marine communities. Relative abundance % (or persistence of occurrence) and % biomass (b.) have been used to identify '1st, 2nd, and 3rd order characterizing species' and 'associated animals' (respective %:% b. ratios 50:5, 50:5, 70:10, and 25:2%) (Thorson 1957). I have used (Lockley 1980*a*, p. 192) relative abundance (%), but not biomass estimates to identify fossil species analogous to modern 'characteristic and associated' species. Pickerill and Brenchley (1979) followed Johnson (1972) in employing a similar, but less quantitative method for identifying characteristic, intergrading, and ubiquitous species.

THE ROLE OF TAXONOMY IN PALAEOECOLOGY

Since the species is the only biologically meaningful taxonomic category, species level taxonomy must be favoured as a basis for defining associations and hence communities. This is particularly true since most Ordovician species have only been defined after rigorous biometric scrutiny. Nevertheless, generic terminology must also be considered, particularly since it has already been employed in a variety of ways.

Species level taxonomy favours biostratigraphic precision and permits differentiation between associations dominated by different species of the same genera. It is useful in the event of taxonomic revisions (which do not affect the species) and, more commonly, in cases where genera like *Dalmanella* are represented by numerous species whose ages and facies preferences differ (cf. Hurst 1979*b*). Species level terminology is also important in rarer cases where congeneric species occur together and there is a need to distinguish their proportions. A further fundamentally important advantage of species level differentiation is that it permits analysis of 'community evolution' by facilitating our understanding of phylogenies.

However, the use of generic abbreviations is less cumbersome and should be considered acceptably accurate providing the following criteria are met: (1) associations should be named unambiguously after constituent species occurring at specified horizons and localities so that there is no doubt about local faunal composition; (2) where a generic category, e.g. *Dalmanella* community, includes a number of associations containing congeneric species, full details of the specific composition, age, and geographical distribution of the association should be given so that all known parts of that compound palaeocommunity are defined equally and adequately.

Since compound palaeocommunities cannot always be named after a single characteristic species, there is a good case for employing species names for association definitions and generic names for palaeocommunities.

KNOWN ANGLO-WELSH ASSOCIATIONS AND PALAEOCOMMUNITIES

Pre-Llanvirn faunas

Shelly brachiopod faunas of Arenig age are known from Anglesey and Dyfed (Bates 1968; Neuman and Bates 1978; Lockley and Williams 1981) and from the Shelve area of Shropshire (Williams 1974, 1976), but have been subjected to only limited palaeoecological analysis. However, it is evident that by early Ordovician (Arenig) times, coarse-ribbed orthaceans (e.g. *Ffynnonia* and *Orthambonites*) had successfully colonized a variety of mainly shallow-water, peri-insular, arenaceous facies associated with 'a group of islands in the middle of the Proto-Atlantic (or Iapetus) ocean' (Neuman and Bates 1978, p. 578; see also Dean 1976, fig. 5). The former authors reiterated Williams's suggestion (1973, p. 249) that such faunas, particularly those from Anglesey, represented a distinct Celtic 'province' associated with the Irish Sea Horst or Geanticline (see also Dewey 1969 and Neuman 1976). However, as similar contemporaneous facies are not well represented elsewhere in Wales and the Welsh Borderland, evidence for a 'distinct' Celtic province is tenuous. Faunal differences probably relate primarily to facies variations. Indeed, Williams (1974, p. 18; 1976, p. 19) noted small representatives of *Orthambonites proava* (Salter), together with *Monobolina plumbea* (Salter) and *Palaeoglossa attenuata* (Sowerby) characterizing silty, even tuffaceous parts of the Arenig Mytton Member (Whittard 1979) whilst a more diverse *Dalmanella* (*D. elementaria*), *Protoskenidioides*, *Euorthisina* association typified contemporary laminated siltstone and shaly facies. This latter association may be related to brachiopod faunas recently discovered from similar facies in Dyfed (R. A. Fortey and R. M. Owens, pers. comm.), and should be differentiated from the sparser inarticulate-dominated faunas here characterized as the *Monobolina* association, which inhabited argillaceous facies also containing trilobites and graptolites (Fortey and Owens 1977).

According to data presented by Williams (1974, table 1) the two Shelve associations may be differentiated as follows:

	Dominant taxa	$\bar{D}$	*NS*	Typical facies
1. *Monobolina* association	*Monobolina* and *Palaeoglossa*	3	19	mudstone
2. 'Diverse' articulate-dominated association	*Dalmanella* *Protoskenidioides*	6	3	siltstone

$\bar{D}$ = Mean Diversity, *NS* = Number of Samples

Although *Monobolina* is clearly the most dominant and persistent form, Williams (1976) included these faunas in the wide-ranging *Pseudolingula* set based on *P. granulata* (Phillips). However, the term is inappropriate since *Pseudolingula* is virtually absent; the assemblages show little taxonomic similarity (clustering), and should at least be differentiated in the manner proposed herein. Co-occurrence of inarticulate and articulate taxa may simply be due to intergrading (ecotones). This generalized contrast between 'an inarticulate association . . . in the finer clastic sediment and a predominantly articulate one . . . in the coarser . . . siltstones . . . or sandstones' (Williams 1974, p. 23) is indicative of patterns recognizable through much of the Ordovician. Cocks and McKerrow (*in* McKerrow 1978, p. 65) referred to an Arenig '*Orthambonites*-crinoid community' characterizing shallow water facies in Dyfed (see Bates 1969). However, since Neuman and Bates (1978, p. 577) considered these assemblages to be specifically and 'significantly different' from penecontemporaneous faunas such as those from Anglesey, this 'community' is simply a generalized means of characterizing the ubiquity of *Orthambonites*.

Llanvirn to Llandeilo faunas

Similar 'facies-fauna' distributions are noted during the Llanvirn. While volcanism persisted in the Builth–Llandrindod complex, the stout, coarse-ribbed orthacean *Hesperorthis* dominated shallow-water arenaceous facies whilst contrasting, sediment-starved, 'offshore' facies were again characterized by inarticulate, trilobite- and graptolite-dominated faunas. Taxonomic observations by Neuman and Bates (1978) that *Orthambonites* of the *Lenorthis* type may be considered 'a subjective junior synonym' of *Hesperorthis* serve to highlight similarities between Arenig and Llanvirn facies faunas.

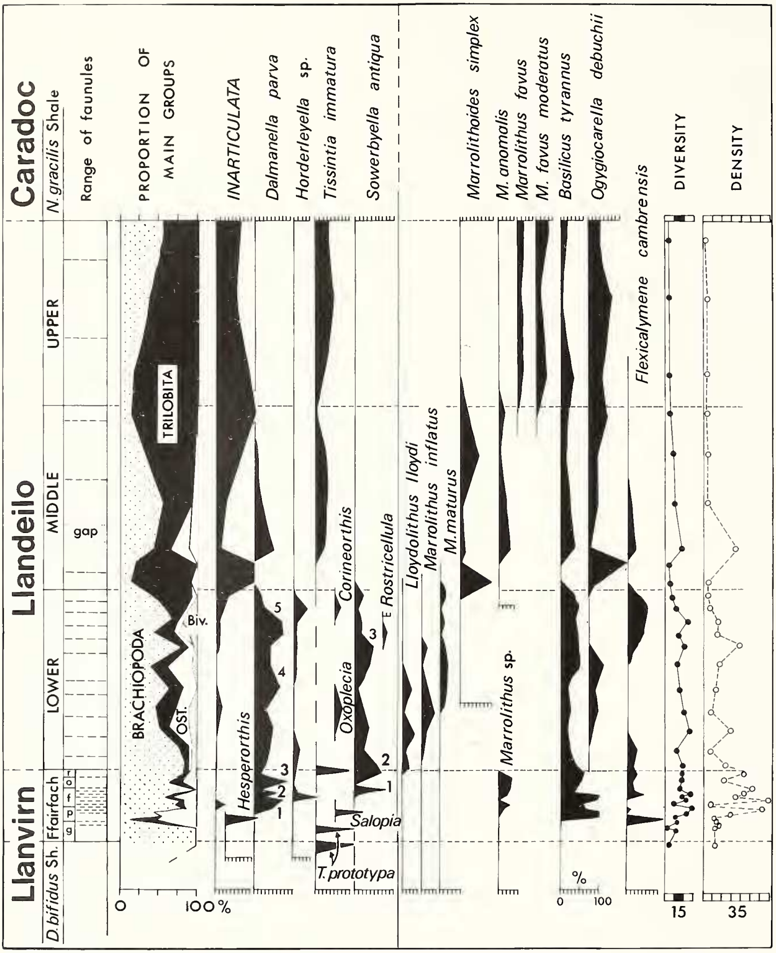
Although Suthren and Furnes (1980) and particularly Furnes (in press) have recently re-evaluated many fossiliferous sedimentary deposits from the Builth area, the conclusions that some coarser *Hesperorthis*-bearing facies represent debris flow or associated fan deposits do not alter the probability of an onshore source. Stratigraphical revisions (Furnes, in press) will alter the nomenclature used in text-fig. 1 and enhance current palaeoenvironmental interpretations.

Contemporaneous finer-grained, silty deposits both here and in the Shelve and Llandeilo areas typically yield *Tissintia* (*T. prototypa* Williams) and *Pseudolingula* (*P. granulata*) forming a distinctive recurrent association (Williams *et al.* 1981; Wilcox and Lockley 1981). Finer, argillaceous, Llanvirn to Lower Caradoc deposits yield, at various horizons, *Obolus*, *Paterula*, *Schizotreta*, *Conotreta*, *Schizocrania*, *Palaeoglossa*, *Lingulella*, *Schmidtites*, *Pseudolingula*, *Tissintia* (*T. immatura* Williams) and *Monobolina* (*M. crassa* Lockley and Williams).

In the Llandeilo area, however, a localized suite of diverse faunal associations is known from sedimentary facies which are texturally intermediate between contrasting orthacean-dominated sandstones and inarticulate-dominated shales. These associations are dominated by articulate brachiopods including *Hesperorthis*, *Salopia*, *Horderleyella*, and in particular *Dalmanella* and *Sowerbyella*. Detailed studies centred on the Llandeilo area (Williams *et al.* 1981; Wilcox and Lockley 1981) indicate that these genera each occupied different habitats circumscribed by highly varied facies distributions. The former three taxa were considered representative of a *Horderleyella* palaeocommunity inhabiting sandy substrates; however, the term *Hesperorthis* palaeocommunity is considered more appropriate because *Horderleyella*-dominated assemblages intergrade with those containing *Dalmanella* and *Sowerbyella* whereas *Hesperorthis* and *Salopia* rarely occur in assemblages containing *Dalmanella* or *Sowerbyella*. Williams *et al.* have shown that both *Dalmanella* (*D. parva* Williams) and *Sowerbyella* (*S. antiqua*), despite co-occurring in some mainly younger assemblages, first appear separately in the succession, show repetitive phases of recurrence, and are more appropriately considered representative of differently structured palaeocommunities. Morphological and taphonomic observations (Williams *et al.* 1981; Wilcox and Lockley 1981) support this contention and tend to conflict with the concept of a generalized *Sowerbyella*–*Dalmanella* community (Cocks and McKerrow: *in* McKerrow 1978).

A summary of the distribution of species in the Ffairfach Group stratotype and succeeding type Llandeilo is given in text-fig. 2, which shows the abrupt faunal changeovers associated with a sequence of rapid Llanvirn facies changes (Williams *et al.* 1981). In contrast, the overlying Llandeilo succession is characterized by a transitional, upward fining facies sequence and corresponding progressive reduction in faunal diversity (Wilcox and Lockley 1981).

Llandeilo faunas from the Shelve area (Williams 1974, tables 6, 7) are dominated initially by *P. granulata*, *P. attenuata*, *Dalmanella salopiensis* Williams, *T. immatura*, and *Rafinesquina delicata* Williams, comprising the trophic nucleus (i.e. 80%; see Neyman 1967) in the silty Meadowtown Member. Subsequently, in the calcareous shales of the Rorrington Member they are dominated by a less diverse inarticulate-dominated fauna characterized primarily by *P. attenuata*, and *D. salopiensis*, with *Schmidtites micula* (M'Coy) and *Lingula displosa* Williams. Clearly this Llandeilo succession is broadly analogous to that recorded in the type area (Wilcox 1979; Wilcox and Lockley 1981) where Lower Llandeilo *Dalmanella parva*-dominated faunules are succeeded by inarticulate-dominated assemblages in the Middle and Upper Llandeilo. It is also interesting to note that Williams (1974, p. 92) considered *D. salopiensis* 'at first sight . . . like the Lower Llandeilo *Dalmanella parva*'. The rare Meadowtown occurrence of *Schizotreta*, *Glyptorthis*, *Kullervo*, and *Murinella* is distinctly reminiscent of similar sporadic occurrences in the *Dalmanella*–*Gelidorthis* association of the Ffairfach Group and the similarities are reflected by a moderate (0·39) coefficient of association (D7/G3 of text-fig. 9 and Table 5). Indeed similarities between Weston, Betton, Meadowtown,



TEXT-FIG. 2. Biostratigraphy of the Ffairfach Group and Llandeilo Series in the type area (faunules based on Williams *et al.* 1981 and Wilcox and Lockley 1981).

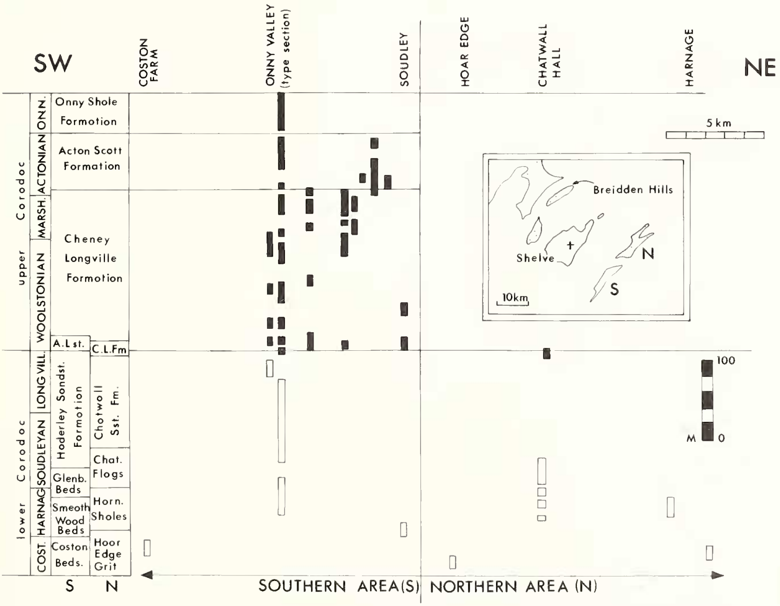
Rorrington, and type Llandeilo faunas are consistently moderate to high (mean coefficient of association $C = 0{\cdot}43$, range 0·23 to 0·64).

McGregor's observation (1961, p. 191) that Upper Llandeilo *Dalmanella* from the Berwyn Hills are conspecific with *D. parva* further substantiates the view that all Llandeilo representatives of this genus are closely related. Amongst the brachiopods and trilobites alone, there are at least twenty species common to both areas (Wilcox 1979, figs. 7, 4–5) and the similarity coefficient ($C = 0{\cdot}58$) is correspondingly high.

Caradoc faunas

Rocks of Caradoc age both in the type area and parts of North Wales are particularly fossiliferous and have therefore been the subject of considerable attention particularly in recent years (Table 1).

(1) *The type area.* Hurst (1979*a*, pp. 185–9) outlined the important contributions made by Bancroft (1929 to 1945) and Dean (1958 to 1964) to our knowledge of the faunal succession in the type area and has himself contributed substantially (Hurst 1978*a*, *b*; 1979*a*, *b*, *c*) to our understanding of this succession. In particular, he formally revised the litho-, bio-, and chronostratigraphy and brachiopod taxonomy for the upper part of the Series (Hurst 1979*a*) and through census sampling of measured sections (text-fig. 3) has identified (1979*b*, *c*) eleven distinctive faunal associations. He



TEXT-FIG. 3. The stratigraphical and geographical distribution of sampled sections in the type Caradoc. Black bars represent sections studied by Hurst (1979*a*, *b*, *c*); white bars represent sections collected by Hurst and currently only partially analysed.

also identified two other 'events' characterized as an 'interregnum' and an 'invasion' (Table 2) and discussed the palaeoecological and evolutionary implications of his conclusions.

TABLE 2. Faunal associations defined by Hurst (1979*b*, *c*) from the upper part of the type Caradoc, listed according to age. N.B. Since Hurst (1979*a*, p. 252) suppressed *B. robusta* as a junior synonym of *B. typa*, his association* should be named after this taxon. *D. lepta* is considered a junior synonym of *D. indica* so again this latter taxon should give its name to the association† (see Cocks 1978)

11	*Onniella broeggeri–Sericoidea homolensis* association	ONNIAN
10	*O. depressa* association	
7b	*O. reuschi–Soerbyella sericea* association (Phase 2)	ACTONIAN
6c	*Dalmanella unguis* association (Phase 3)	
9	*Leptestiina oepiki* association	
8	*O. reuschi–Chonetoidea radiatula* association	
7a	*O. reuschi–S. sericea* association (Phase 1)	MARSHBROOKIAN
6a, b	*D. unguis* association (Phases 1 and 2) (*D. wattsi* invasion)	
5	*D. multiplicata–S. sericea* association	
4	*Kjaerina typa* association	WOOLSTONIAN
3b	*B. typa* association (Phase 2)* (*Heterorthis alternata* interregnum)	
3a	*B. typa* association (Phase 1)*	LONGVILLIAN
2	*D. indica* association†	
1	*Howellites antiquor* association	

Although reminiscent of the older zonal categories of Bancroft (1933, 1945), these associations were defined using rigorous quantitative biostratigraphical procedures and, as such, are directly comparable to other similarly defined associations (Lockley 1980*a*; Williams *et al.* 1981).

However, despite acquiring substantial Lower Caradoc collections from relatively widely separated sections (text-fig. 3), Hurst was unable to complete their analysis and reported (1979*a*, p. 185) that I had inherited the material. This is now housed mainly in the British Museum (Natural History) and the new forms which have been discovered are presently being studied for future description.

Since current studies of the type Lower Caradoc are incomplete, we must rely on Dean (1958), Williams (1973), and Pickerill and Brenchley (1979) for up-to-date, albeit brief, interpretations of the faunal succession. Table 3 shows the biostratigraphical subdivisions proposed by Dean, Williams, Brenchley, and Pickerill in the most recent relevant publications. Note that Dean's classification reflects Bancroft's Correlation tables (1933) and that zones 8b and 8c are now reflected by Hurst's associations.

Since Hurst (1979*a*, *b*, *c*) completed his studies of the type Caradoc, the Onny Valley road (A489) has been widened creating continuous exposures of the Cheney Longville Formation. This has provided Drs. P. J. Brenchley and G. Newall with an opportunity to reassess both the facies and fauna. They report (pers. comm. and MS) that the sedimentary succession is not a simple fining upwards sequence (cf. Hurst 1979*b*) but rather exhibits alternating sandstones and mudstones of a shallow subtidal environment influenced by the periodic development of wave-affected sand lobes. They also confirm that the mudstones contain a low-density, *Kjaerina*-dominated background fauna which contrasts with the more variable, transported faunas of the sandstone units. They consider, therefore, that the faunal associations differentiated by Hurst (1979*b*) show considerable intergradation and even contain hitherto unrecorded elements like *Nicolella*.

Cocks and McKerrow (*in* McKerrow 1978) outlined two communities based partly on type Caradoc faunas. The first, the *Sowerbyella–Dalmanella* community, is more generalized and apparently encompasses pre-Caradoc faunas in which these genera dominate. The second, the

TABLE 3. Biostratigraphical subdivisions of the type Lower Caradoc

BIOSTRATIGRAPHICAL SUBDIVIDIONS				
Stage	Modified after Dean (1958, text-fig. 3)		After Williams (1973, text-fig. 1)	After Pickerill (1979) and Brenchley and Pickerill (1980)
LONGVILLIAN	8c	*Bancroftina typa*		
	8b	*Dalmanella indica*		
	8a	*D. horderleyensis*		
SOUDLEYAN	7	*Reuschella horderleyensis* and *Broeggerolithus soudleyensis*	*Dinorthis* association	*Dinorthis* community
	6	*Onniella avelinei* and *Broeggerolithus broeggeri*		
HARNAGIAN	5	*Salterolithus* (*Ulricholithus*) *ulrichi*	*Onniella* association	
	4	*S. caractaci*		
	3	*Smeathenella harnagensis*, *Salopia salteri*, *Reuscholithus reuschi*, and *Salterolithus smeathenensis*		
COSTONIAN	2	*Horderleyella plicata* and *Costonia ultima*	*Dinorthis* association	*Dinorthis* subcommunity
	1	*Harknessella vespertilio* and *Dinorthis flabellulum*		

Dinorthis flabellulum community, refers more specifically to existing classifications (cf. Table 3). Although both were described briefly for the benefit of the non-specialist student, and as such contain only selected detail, recent studies (Table 1) add new and significant information.

As stated above, *Sowerbyella* and *Dalmanella* are often mutually exclusive in older (Llanvirn) associations and, in the Llandeilo (Wilcox and Lockley 1981), had their distributions at least partially controlled by transportational processes. In the type Caradoc (Table 2) their co-occurrence locally warrants the naming of a *Dalmanella–Sowerbyella* association (Hurst 1979*b*) although elsewhere *Sowerbyella* occurs more abundantly with the other dalmanellids *Bancroftina*, *Howellites*, and *Onniella*. The differentiation noted in the Llanvirn never entirely breaks down, and in the Llandeilo and Caradoc (Williams 1974; Lockley 1980*a*) *Sowerbyella* frequently occurs independently in characteristic 'Bursts' first noted by Bancroft (1945). Cocks and McKerrow (*in* McKerrow 1978, p. 80) also included *Kjaerina* and *Oxoplecia* as distinctive representatives of their community. Whilst this may be true of *Kjaerina*, which now gives its name to Hurst's association (No. 4 of Table 2), *Oxoplecia* is unknown in the Caradoc; its closest relative (Williams 1974) is *Bicuspina*, which was rare in late Caradoc times in the type area (Hurst 1979*b*) and is in need of paleoecological documentation for the type area in early Caradoc times. It is surprising that Cocks and McKerrow did not refer to the original associations of Williams (1973) on his work on *Dalmanella* and *Sowerbyella* phylogenies (1976). Recently Hurst has further explored the phylogeny of *Dalmanella* and other dalmanellids.

The Caradoc *Dinorthis flabellulum* community outlined by Cocks and McKerrow (*in* McKerrow 1978, p. 78) as a fauna in which 'only . . . *Dinorthis* and *Harknessella* were at all common', was first characterized by Williams (1973, p. 242) as an association 'with *Biscuspina*, *Dalmanella*, *Heterorthis*, and *Leptaena*'. Such brief and vague descriptions are unsatisfactory and reflect poor definition of the *Dinorthis* community; this poor delineation is reaffirmed by the cluster analysis (text-fig. 10), which reveals only a low correlation ($C = 0{\cdot}29$) between *Dinorthis* faunas from Shropshire (C_4) and North Wales (C_2). Pickerill and Brenchley (1979) have shown that *Heterorthis* may comprise 25–53% of the community whilst other forms occur locally in significant proportions. There is also no documentation to support the assertion (Cocks and McKerrow: *in* McKerrow 1978, p. 78) that 'the inarticulate brachiopods were represented by the lingulid *Palaeoglossa*'; this genus is almost invariably associated with facies in which the *Dinorthis* community is largely or totally unrepresented.

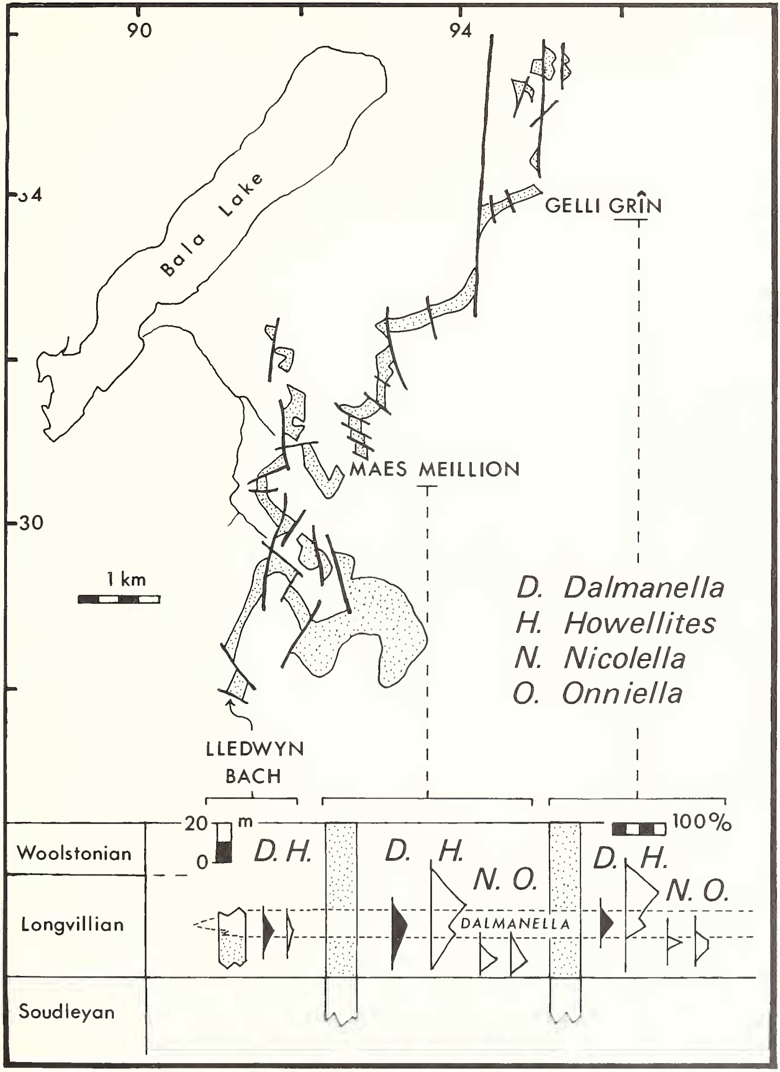
(2) *Caradoc faunas of North Wales*. Since Williams (1963, 1973), Bassett, Whittington and Williams (1966), and Whittington (1962–1968) completed a major phase of research on the Lower Bala Group (Costonian to Longvillian), further studies in the Bala and adjacent Berwyns area (see Table 1) have largely focused on analysis of the faunal associations outlined by Williams (1973). Pickerill and Brenchley (1979, p. 230) 'adopted' the associations of Williams (1973), which they recognized in the Berwyns area and 'elevated to community rank'. Apart from giving a quantitative outline of the relative abundance (%) and persistence of occurrence (presence %) of genera at studied localities and subdividing their *Dinorthis* community into a *Dinorthis* and a *Macrocoelia* subcommunity, perhaps their most novel contributions were the recognition of a *Dalmanella* community in North Wales, and the presentation of palaeoenvironmental interpretations.

Although I have commented (Lockley 1980*a*, p. 228) on the similarity ($\bar{C} = 0{\cdot}73$, range 0·63 to 0·84) between the *Dalmanella*, *Howellites*, and *Dinorthis* communities in the Berwyn areas, the restricted stratigraphical occurrence of the *Dalmanella* community (Pickerill and Brenchley 1979, text-figs. 5, 6, 8) enhances potential for precise correlations. The 'local association containing *Dalmanella Leptestiina* and *Howellites*' in the Gelli-grîn Formation south of Bala (Lockley 1980*a*, p. 184) is evidently indicative of the temporary development of a *Dalmanella*-dominated association (text-fig. 4) representing a transitional stage between the *Nicolella–Onniella* and *Howellites–Kloucekia* associations (*sensu* Lockley 1980*a*). The younger Longvillian *Dalmanella* (*D. indica*)-dominated faunas of the Berwyns region (Pickerill and Brenchley 1979, text-fig. 6) are probably contemporaneous with this Bala association characterized by *D. modica*, a species considered 'superficially like *D. indica*' (Williams 1963, p. 385). Such an interpretation accords with Pickerill and Brenchley's observations (1979, text-figs. 5, 6) on the diachronism of Longvillian facies and implies that older Longvillian *D. horderleyensis* zone faunas from the Berwyns region are probably coeval with the oldest Gelli-grîn faunas from Bala, characterized as the *Nicolella–Onniella* association (Lockley 1980*a*). Similarly, such correlations would emphasize the affinities between upper Longvillian (Woolstonian of Hurst 1979*a*) faunas from the Pen y Garnedd Limestone Formation and the 'Bala' Cymerig Limestone Member. It is worth noting the statistically significant taxonomic similarities ($C = 0{\cdot}24$–$0{\cdot}39$) between the *Leptestiina oepiki* association of Shropshire (E_{12} of text-fig. 9), the Gelli-grîn faunas (B_5), the *Nicolella* community of the Berwyns (C_6), and the *Bicuspina* set of the Whittery shales (D_{15}). Since such diverse *Nicolella* palaeocommunity faunas are considered to have arisen from pre-Caradoc *Dalmanella*-dominated faunas it is not surprising that species of *Dalmanella* locally dominate by a 2 : 1 ratio (Williams 1974, table 8; Lockley 1980*a*, fig. 12). However, the term *Dalmanella* palaeocommunity is best reserved for type Marshbrookian associations where the genus consistently dominates in greater proportions (Hurst 1979*b*).

Shelve faunas

Material collected by Whittard and studied by Williams (1974, 1976) could not be subjected to the same biostratigraphically and quantitatively precise analysis afforded material from most other areas. Consequently Williams (1976) employed the 'non-committal' term 'set' when grouping the useful quantitative data presented in his monograph (1974).

It has already been shown that the term '*Pseudolingula* set' should either be abandoned or, where appropriate, supplanted by the term '*Tissintia–Pseudolingula* association'. The term '*Bicuspina* set' is also of limited value and essentially a junior synonym of the term *Nicolella* association (Williams 1974, pp. 22, 23; Pickerill and Brenchley 1980). This similarity may be substantiated quantitatively



TEXT-FIG. 4. The stratigraphical and geographical distribution of *Dalmanella* (*D. modica* Williams) in the Gelli-grîn Formation (stippled) of the Bala area; data modified after Lockley (1980*a*, *b*).

(text-fig. 9); respective mean *C* values of 0·37 (range 0·26–0·50) and 0·29 (0·22–0·36) indicate a moderate association between Shelve faunas and those from Bala and the Berwyns. *Bicuspina* is only recorded abundantly at two Shelve horizons (Williams 1974, tables 8 and 11) and in the Gelli-grîn Formation (Lockley 1980*a*), and in both areas *Bicuspina*, *Reuschella*, and *Onniella* rank amongst the five most abundant and ubiquitous genera.

It is not surprising that the Hagley Shale faunas are reminiscent of the *Onniella–Sericoidea* association (cf. Hurst 1979*b*; Lockley 1980*a*) since such faunas are commonly associated with those containing *Nicolella*.

Finally, the *Lingulella* set appears to be a useful concept. Not only does this genus and/or *Palaeoglossa* (its close relative and possible junior synonym; Williams 1974) characterize a number of known faunas from fine-grained facies, but they fall into a recognizable taxonomic cluster (text-fig. 10).

Representative shelly faunas from Dyfed

Addison's studies (1974) on the Llandeilo to Caradoc faunas of Dyfed indicate the presence of a suite of little-known, yet diverse assemblages in strata assigned to the 'Narbeth Group' (see Bassett, Ingham and Wright 1974, fig. 7). Consequently, following the publication of Addison's more important regional stratigraphical conclusions (*in* Williams *et al.* 1972, and *in* Bassett *et al.* 1974), a detailed census sample study of this group was undertaken, based on the Lampeter Velfrey section (see Addison 1974, text-figs. 28, 30; Bassett *et al.* 1974, fig. 7). Preliminary results are summarized here in text-fig. 5, which shows the distribution of brachiopod taxa (species) in the most arenaceous part of the section, the 'Bryn Sion Sandstone Member'. These results are important since the section has since been partially covered and because they highlight the facies 'preference' of *Heterorthis*, which elsewhere is also commonly associated with arenaceous facies. Other heterorthids (e.g. *Tissintia* and *Heterothina*) also represent important or virtually monospecific constituents of the fauna elsewhere in this succession (Addison 1974) and particularly in South Wales appear to have enjoyed a degree of early to mid Ordovician proliferation rivalled only by the contemporary and subsequent success of the closely related dalmanellids.

Ordovician faunas from south-west England

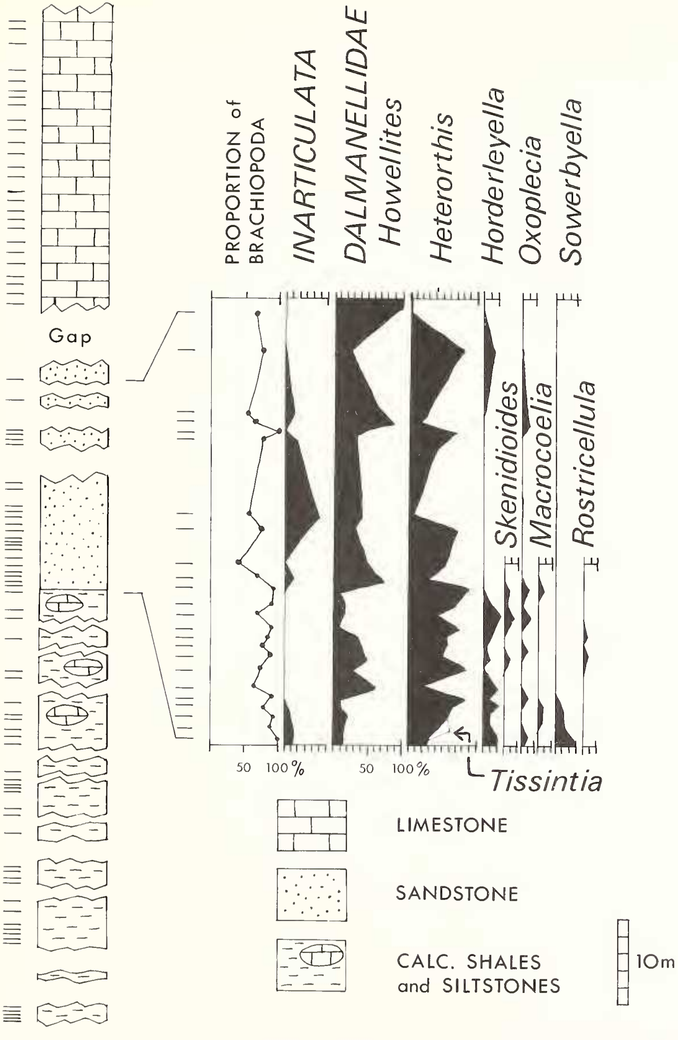
A reasssessment of the brachiopod faunas from the Budleigh Salterton pebble bed (Cocks and Lockley 1981) has shown that the dominant species, the small orthide commonly known by the specific name *budleighensis* Davidson is in fact a heterorthid recognized by Havlíček (1970) as a representative of the genus *Tafilaltia*. This largely monospecific occurrence in association with an arenaceous facies, also locally containing *Corineorthis*, *Salopia*, and ?*Hesperorthis* is noteworthy because it is also reminiscent of contemporary Welsh associations.

SYNTHESIS

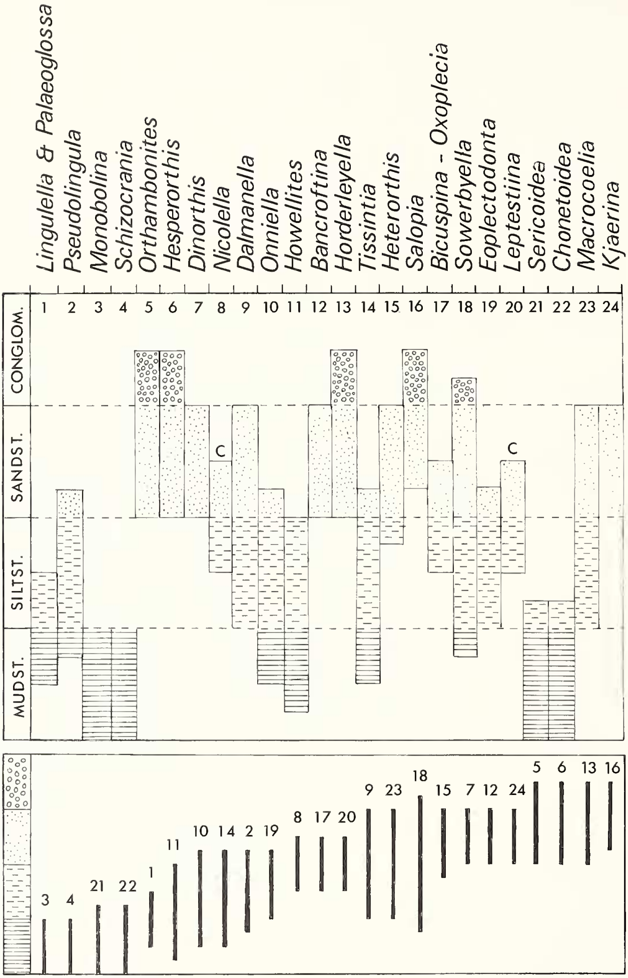
General models

Evaluating the significance of the associations and communities outlined above, which, excluding obvious synonyms, number about thirty, can be approached with the type of 'matrix' presentation shown in text-fig. 6. Although there are some shortcomings, such as the inevitably generalized textural classification of sediments which results from synthesizing the observations of palaeontologists, certain clear patterns do emerge. At the coarser end of the textural spectrum, facies are dominated by coarse-ribbed orthaceans (e.g. *Hesperorthis* and *Dinorthis*) together with forms like *Heterorthis*, *Tafilaltia*, *Salopia*, and the dalmanellid *Bancroftina*, whilst in finer-grained argillaceous facies inarticulate brachiopods are dominant and articulates represented only by plectambonitacean aegiromenids such as *Sericoidea* and *Chonetoidea*.

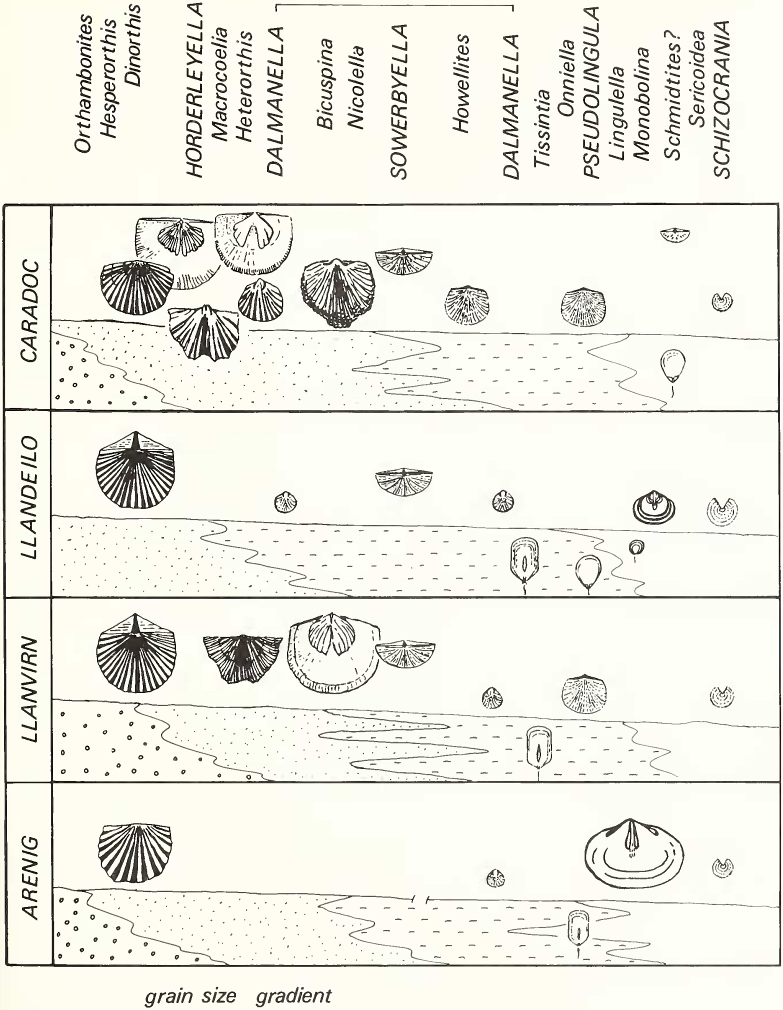
The silty middle part of the facies spectrum is dominated largely by dalmanellids, related heterorthids (e.g. *Tissintia*), and the larger plectambonitaceans (e.g. *Sowerbyella*), all of which appear to be eurytopic in their relatively wide facies ranges (text-fig. 7).



TEXT-FIG. 5. The distribution of dominant Brachiopoda in the arenaceous Bryn Sion member of the Narberth Group at Lampeter Velfry.



TEXT-FIG. 6. Apparent facies ranges of brachiopod genera representing named associations (and/or palaeocommunities) discussed in text. Facies ranges cannot be defined precisely in terms of grain size (Ø scale) so arbitrary quartiles are used to suggest range of taxa into fine, medium, or coarser textural spectra. The taxonomic classification (1–24) is rearranged in lower box to show distribution of taxa in relation to facies gradient.



TEXT-FIG. 7. Facies relationships of key brachiopods throughout the Ordovician showing consistent 'preferences' of some taxa.

This simple, threefold division serves as a useful preliminary model for further scrutiny and refinement. The obvious facies-fauna relationships highlighted by this summary (text-figs. 6, 7) indicate the urgent need for greater understanding of the entombing sedimentary facies. Despite attempts by Hurst (1979*b*, *c*), Pickerill and Brenchley (1979), and Wilcox and Lockley (1981) to broaden our understanding of Ordovician facies by using generalized sedimentological observations to present environmental reconstructions, no thorough sedimentological studies have been undertaken on the facies under discussion. None has even been defined in terms of standard textural (Ø scale) or mineralogical classifications and as such may be wrongly categorized. For example, the apparently equable distribution of sandstones, siltstones, and mudstones shown in text-fig. 6 hardly conforms with normal distributions seen in nature (Shea 1974) and probably implies that the extent of sandy, particularly medium 1-2 Ø sandstone facies has been underestimated. Furthermore, varying degrees of textural inhomogeneity are also inevitably masked by simplistic classifications. Although such subtle sedimentological variation may elude the palaeontologist it is undoubtedly of considerable significance to benthic organisms and as such should warrant more detailed study.

Despite these shortcomings, a growing volume of data on relationships between facies and fauna continues to enhance our understanding of Ordovician palaeoenvironments and suggest the need for appropriate interpretations. Pickerill and Brenchley (1979, p. 260) suggested comparisons between certain Silurian communities and inferred, facies-related Ordovician analogues from North Wales. They proposed (p. 229) that the apparently relatively shallow depth ranges (0-30 m) for these Ordovician communities might suggest . . . 'that benthic faunas progressively migrated into deeper waters throughout the Lower Palaeozoic', a popular idea which appears to reiterate the suggestion of Cocks and McKerrow (*in* McKerrow, 1978, p. 62) that there was a 'gradual colonization of deeper environments by the brachiopods'.

These suggestions presuppose that Ordovician communities are accepted as analogues of Silurian counterparts, when in fact little detailed taxonomic or ecological comparison has been attempted. Comparison of the two pairs of proposed analogues (see Table 4) indicates minimal taxonomic similarity; only a few of the dominant constituents even belong to the same order and none are well-recognized homoeomorphs. Hurst and Watkins (1981) independently noted that 'taxonomically' other potentially comparable Ordovician and Silurian communities were 'vastly different'.

Pickerill and Brenchley used Boucot's (1975) Benthic Assemblage concept to equate these communities on the primary assumption that they inhabit similar hatitats. Although detailed evidence for such assumptions is tenuous, comparisons of inferred habitats of palaeocommunities (as in text-fig. 7) obviously has potential, *providing* that palaeoenvironments are correctly inferred from sedimentary facies. It should be remembered that such comparisons ignore the possibility that the considerable differences reflect differential preservation of various shoreface and open-shelf deposits in the type successions. Since many of the Ordovician faunas discussed herein derive from deposits associated with insular volcanic centres (text-figs. 1, 8) it seems prudent to be cautious of a model which implies any great similarity between Ordovician and Silurian Welsh Basin environments. Direct comparisons seem most feasible only in the vicinity of the south-east margin of the basin, where similar Ordovician and Silurian shelf deposits occur (Hurst and Watkins 1981).

Quantitative summary

The most rational approach to a quantitative synthesis of described faunal associations (and palaeocommunities) is to compare the proportion of taxa in common throughout the whole spectrum of described faunas. This is done by cluster analysis using the data presented in Table 5 and text-fig. 9.

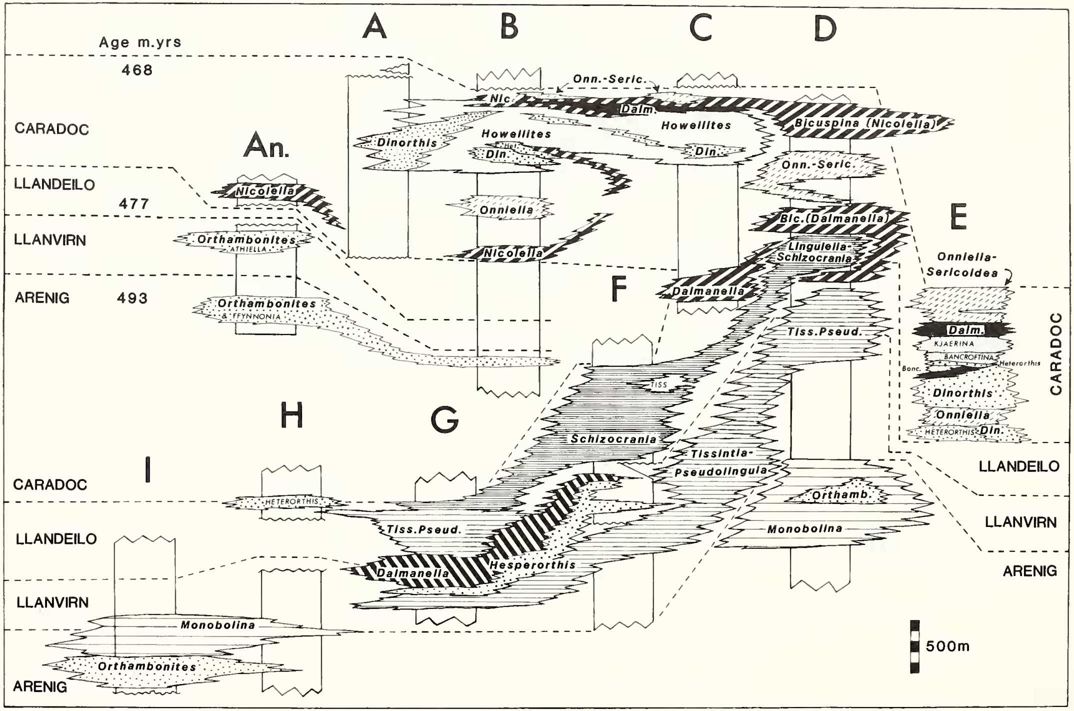
The first step involves identifying all recorded taxa and the associations in which they occur; Table 5 shows that species representative of some 124 genera occur in the fifty-eight representative Welsh associations listed A_1-H_1. Cross comparison of the composition of all these faunas using Dice's formula $2C/(N_1+N_2)$ (see Whittington and Hughes 1974, p. 204), where C represents

TABLE 4. Dominant genera in supposedly analogous Ordovician (*left*) and Silurian (*right*) communities from Wales and the Welsh Borderland (data from Pickerill and Brenchley 1979, tables 4, 7; and Ziegler, Cocks and Bambach 1968, figs. 3, 7). Dominant forms comprising 80% of these communities (i.e. the Trophic Nucleus *sensu* Neyman 1967) rarely belong to the same groups; e.g. in the *Dinorthis-Eocoelia* comparison only 11% are common to the same family, the ubiquitous Dalmanellidae, whilst in the *Nicolella-Costricklandia* comparison none even belong to the same order.

ORDOVICIAN		SILURIAN	
Dinorthis community		*Eocoelia* community	
	%		%
Heterorthis	53	*Eocoelia*	47
Howellites	11	'*Camarotoechia*'	18
Reuschella	4	*Dalejina*	12
Dinorthis	8	*Strophochonetes*	9
Sowerbyella	13		
	—		—
	89 = Trophic nucleus		86
Nicolella community		*Costricklandia* community	
	%		%
Nicolella	34	*Costricklandia*	49
Dolerorthis	21	*Pholidostrophia*	14
Platystrophia	16	*Eocoelia*	11
Skenidioides	9	*Eospirifer*	7
	—		—
	80		81

conspecific (1·0) or congeneric (0·5) taxa in common and N_1 and N_2 the number of species in compared assemblages, yielded 1653 coefficient of association values (text-fig. 9). The sample size represented by so many permutations is sufficiently large to generate a histogram and curve exhibiting a classic negative exponential pattern. The principles of probability theory can be used to assess the significance of these values; if 25% is chosen as the minimum confidence level then only C values of 0·19 or more can be considered to depart significantly from zero; values equal to or greater than 0·33, 0·45, and 0·68 respectively would correspond to the 10%, 5%, and 1% confidence limits. These constraints allow the C values to be ranked as insignificant, low, moderate, high, or very high (text-fig. 9).

A dendrogram constructed from the matrix data (text-fig. 10) clearly highlights the similarity between many related associations and provides quantitative substantiation of many authors' more qualitative observations and predictions. Indeed the taxonomically related subclusters also reflect age, close geographical relationships, and facies preferences and are therefore of great value in defining the major palaeocommunity groupings (I–VIII) outlined below. For example, the Soudleyan *Howellites* community of the Berwyn Hills area (Pickerill and Brenchley 1979), although similar to the contemporaneous *Howellites-Paracraniops* association, is hard to differentiate from the Berwyns *Dinorthis* community. The North Wales (Berwyns) *Dinorthis* community bears little relationship to the *Dinorthis* community in Shropshire. Such observations suggest that the term



TEXT-FIG. 8. Stratigraphical and geographical distribution of named associations (and/or palaeocommunities) in the Ordovician of Wales. Areas A–I as in text-fig. 1; An = Anglesey; biostratigraphical subdivisions in areas E and G have been further refined. Scale of section E doubled.

'*Dinorthis* community' is problematical and should provisionally be restricted to description of the Shropshire faunas, while the North Wales expression of this fauna should be regarded as limited, intergrading into the dominant *Howellites* community.

The Longvillian faunas of the Bala area cluster together and are closely related to contemporaneous faunas from the Berwyns and Shelve areas, all of which show high *C* values and bear some relationship to the *Nicolella* association. This predominantly North Wales cluster is most closely related to type Caradoc faunas from Shropshire which, with the exception of the distinctive Onnian faunas, all form a discrete cluster exhibiting high *C* values. These Caradoc faunas fall into age-differentiated subclusters dominated successively by the dalmanellids *Bancroftina*, *Dalmanella*, and *Onniella*. Remaining Caradoc faunas (C_4, A_2, B_1, E_{13}, and E_{14}; text-fig. 10) exhibit low to moderate *C* values.

Pre-Caradoc faunas all fall into an entirely separate cluster which is less clearly subdivided. However, three distinct subcluster groupings are evident; the first approximates closely to the *Lingulella* set of Williams (1976) and includes one of only two 'anachronistic' (i.e. post-Caradoc) faunas in the entire cluster; the second subcluster is dominated by *Hesperorthis*, whilst the third includes *Dalmanella*-, *Horderlyella*-, and *Sowerbyella*-dominated associations from the Ffairfach Group. It is worth emphasizing the distinction between these latter two groupings since it largely justifies the suggested re-evaluation of groupings proposed by Williams *et al.* (1981).

Most remaining faunas in the pre-Caradoc subcluster bear some relationship to the Shelve inarticulate faunas or the mid-Wales *Tissintia–Pseudolingula* faunas described by Williams *et al.* (1981) and Wilcox and Lockley (1981). High *C* values indicate that the latter faunas are more closely associated with the main clusters than the Shelve Group, which exhibit mainly moderate to low *C* values. Such observations substantiate the view that the term '*Pseudolingula* set' should be abandoned.

Cluster analysis provides a valuable method of comparing the taxonomic composition of faunas throughout the whole spectrum of described associations, palaeocommunities, and other representative groupings. It furnishes us with an unequivocal picture of the taxonomic interrelationship between faunas and strongly corroborates previous subjective observations by providing precise quantitative comparisons (*C* values). Used in conjunction with probability theory these values are more than sufficient in number to permit the development of a confidence-limited scale objectively defining insignificant, low, moderate, high, and very high degrees of association (*C*).

Despite the obvious advantages derived from thorough quantitative comparisons there are two obvious limitations. First, cluster analysis does not take into account the relative abundance of taxa in compared samples. As stated in the introduction to this review, many associations or palaeocommunities are named after their dominant constituents, which may make up a large proportion of the trophic nucleus. Unfortunately, cluster analysis weights rare elements equally so that two faunas showing a low *C* value at the trophic nucleus level (i.e. comparison of dominant 80%) might, having rarer elements in common, show a high *C* value when fully compared. Despite this drawback, full analysis can be very useful since it will help to identify intergrading between associations from the same geographical area. The *Howellites* and *Dinorthis* communities of the Berwyn Hills in North Wales provide a good example of faunas which are differentiated on the basis of relative proportions but have overall taxonomic similarities attributed to intergrading (Pickerill and Brenchley 1979). As shown, the same is true for some of the Ffairfach Group associations. (Allied to this problem of species proportions is the whole issue of non-brachiopod faunas. However, this is of no direct concern here since virtually all recorded type Ordovician associations are named after brachiopods and are accompanied by full lists of proportions of non-brachiopod elements.) Secondly, cluster analysis cannot take account of facies variation, which most authors agree has a very important bearing on the distribution of faunas. Again, the Ffairfach Group provides examples of associations like those dominated by *Horderleyella* and *Dalmanella*, which although similar in taxonomic composition not only show pronounced variation in species proportions but also exhibit quite distinct facies preferences. Nevertheless, as stated above, the taxonomic clusters often reflect similar facies preferences amongst related assemblages.

Bearing these three important criteria of taxonomic compositions (*C* values), species proportions, and facies relationships in mind, a final assessment of palaeocommunities is possible.

Perspective on palaeocommunities

Known pre-Upper Llanvirn faunas from Anglesey and Shelve show no significant taxonomic relationship discernible with present data. Even within the Shelve area *C* values are generally only moderate and the all-embracing term '*Pseudolingula* set' is abandoned in favour of the categories proposed here (text-fig. 8) and elsewhere (Williams *et al.* 1981; Wilcox and Lockley 1981).

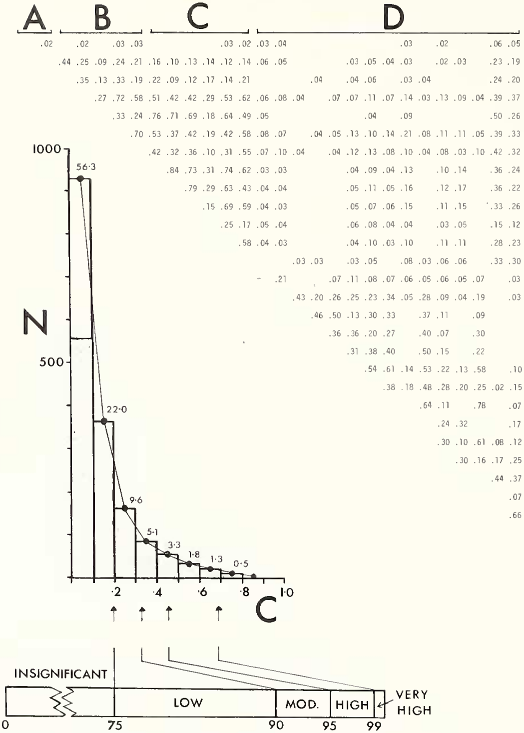
The development of the Llanvirn *Tissintia*–*Pseudolingula* association closely coincides with the establishment of other consistently recognizable faunas, in particular those dominated by *Dalmanella*. These fall into a number of categories (Williams *et al.* 1981) whose relationships are only partially understood. Even where the best quantitative biostratigraphical data are available, problems hinge primarily on deciding which of the three fundamental criteria are most important. For example, is the *Horderleyella* association related to the *Salopia* and *Hesperorthis* associations from similar facies? Or on the basis of taxonomic composition, does it bear a closer resemblance to *Dalmanella* associations (text-fig. 10)? Although Williams *et al.* (1981) named a *Horderleyella* palaeocommunity, the latter hypothesis is favoured here. Indeed, as the *Horderleyella* association becomes less distinctive with time so the *Dalmanella* and *Sowerbyella* palaeocommunities (Williams *et al.* 1981) intergraded more in the less differentiated facies of the type Llandeilo. Elsewhere,

TABLE 5. Distribution of taxa (genera 1–124) in representative faunas from Wales and the Welsh Borderland.

Genera are as follows: 1, *Ahtiella*, *Anisopleurella*, *Antigonambonites*, *Apsotreta*, *Astraborthis*, *Atelelasma*, *Bancroftina*, *Bellimurina*, *Bicuspina*. 10, *Bilobia*, *Bimuria*, *Bystromena*, *Caeroplecia*, *Camerella*, *Chonetoidea*, *Christiania*, *Clitambonites*, *Conotreta*, *Corineorthis*. 20, *Cremnorthis*, *Cryptothyris*, *Cyclospira*, *Cyrtonella*, *Dactylogonia*, *Dalmanella*, *Desmorthis*, *Destombesium*, *Diaphelasma*, *Dinorthis*. 30, *Diparelasma*, *Dolerorthis*, *Drabovia*, *Elliptoglossa*, *Eocramatia*, *Eoplectodonta*, *Estlandia*, *Euorthisina*, *Ffynnonia*, *Furcitella*. 40, *Gelidorthis*, *Glossorthis*, *Glyptomena*, *Glyptorthis*, *Harknessella*, *Hedstroemina*, *Hespernomia*, *Hespernomiella*, *Hesperorthis*, *Heterorthina*. 50, *Heterorthis*, *Horderleyella*, *Howellites*, *Ilmarinia*, *Kïaromena*, *Kjaerina*, *Kjerulfina*, *Kullervo*, *Leptaena*, *Leptestiina*. 60, *Lingulasma*, *Lingulella*, *Lingulops*, *Macrocoelia*, *Marionites*, *Mcewanella*, *Metacamerella*, *Monobolina*, *Monorthis*, *Murinella*. 70, *Nicolella*, *Nocturniella*, *Obolus*, *Onniella*, *Orbiculoidea*, *Orthambonites*, *Orthis*, *Orthisocrania*, *Oslogonites*, *Oxoplecia*. 80, *Palaeoglossa*, *Palaeostrophomena*, *Paracraniops*, *Parastrophinella*, *Paterula*, *Paurorthis*, *Petrocrania*, *Plaesiomys*, *Platystrophia*, *Plectorthis*. 90, *Porambonites*, *Productorthis*, *Protoskenidioides*, *Protozyga*, *Pseudolingula*, *Ptychoglyptus*, *Ptychopleurella*, *Rafinesquina*, *Rectotrophia*, *Reinversella*. 100, *Reuschella*, *Rhactorthis*, *Rhynchorthis*, *Rhynchotrema*, *Rostricellula*, *Rugostrophia*, *Salacorthis*, *Salopia*, *Schizocrania*, *Schizotreta*. 110, *Schmidtites?*, *Sericoidea*, *Skenidioides*, *Sowerbyella*, *Strophomena*, *Taffia*, *Tazzarinia*, *Tissintia*, *Treioria*, *Trematis*. 120, *Triplesia*, *Tritoechia*, *Vellamo*, *Whittardia*, *Zygospira*.

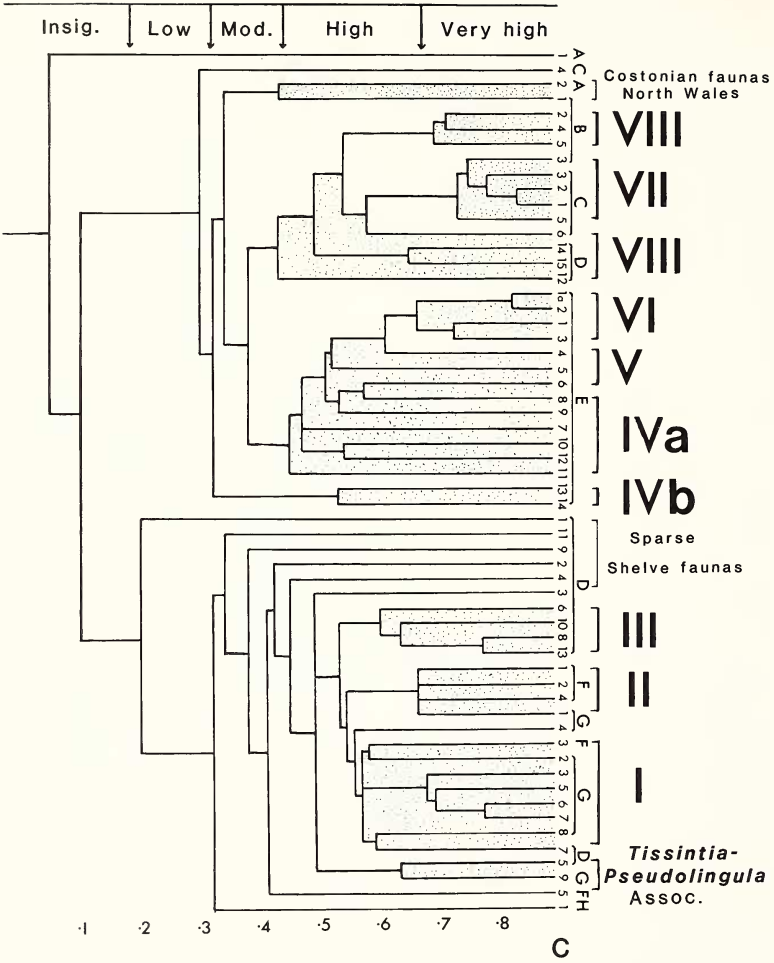
Faunal assemblages, associations, and other groupings used in cluster analysis: (text-figs. 9, 10) A_{1-2} respectively pre-Costonian and Costonian Anglesey faunas after Bates 1968 (revised by Neuman and Bates 1978), B_{1-5} Caradoc faunas from the Bala area respectively characterized as the *Nicolella*–*Onniella* association (Phases 1 and 2), the *Howellites*–*Paracraniops* association, the *Howellites*–*Kloucekia* association, and the *Onniella*–*Sercoidea* association after Lockley (1980*a*; supplementary data from Whittington and Williams 1955 and Williams 1963); C_{1-6} Caradoc faunas from the South Berwyn Hills respectively characterized as the *Howellites* community, the *Dinorthis* and *Macrocoelia* subcommunities, the *Dinorthis* community (Shropshire), the *Dalmanella* and *Nicolella* communities; D_{1-15} Faunal assemblages from the Shelve area after Williams (1964) with subdivisions proposed by Williams (1976); $E_{1,\,1a,\,2-14}$ Upper Caradoc associations from the type area, Shropshire, after Hurst (1979*a*, *b*, *c*). (E_1 and $_{2-14}$ after Hurst 1979*b*, table II with supplementary data from Hurst 1979*a*; E_{1a} after Hurst 1979*c*); F_{1-5} Llanvirn faunas from the Builth area, respectively collections BW 10, BW 11, BW 13, NMW.68.376G. 150–161 after Williams *et al.* (1981 tables 3, 4), and *Tissintia*–*Pseudolingula* fauna from Camnant Brook (Lockley and Williams 1981, p. 46); G_{1-7} respectively Llanvirn faunas from the Llandeilo area characterized as the *Hesperorthis*, *Salopia*, *Dalmanella*–*Gelidorthis*, *Schizocrania*, *Dalmanella* (3 phases), *Horderleyella*, and *Sowerbyella* (2 phases) associations of Williams *et al.* (1981); G_8 and G_9 respectively Lower to early Middle and Middle to Upper Llandeilo faunas (Wilcox 1979; Wilcox and Lockley 1981); H_1 Bryn Sion faunas of the Narberth group (text-fig. 5 herein).


A
B
C
D
E
F
G
H
20
40
60
80
100
120



TEXT-FIG. 9. Cluster analysis matrix, resultant histogram, and scale of *C* values derived from comparison of fifty-eight representative faunas listed in Table 6; blank parts of histogram and matrix represent zero values. (See text for further details.)

	E															F					G									H
A						.03	.03		.02		.02		.03					.03							.03			.03		.03
	.03	.05	.06	.03		.06	.05	.06	.09	.03	.06	.08	.10	.09	.06			.06	.03			.09	.10	.03	.05	.06	.09	.05	.03	.06
B	.08	.06	.07	.13	.03	.04	.03	.04	.08	.03	.07	.10	.09	.16	.13			.04				.08	.09		.03	.04	.07			.07
	.10	.19	.18	.11	.13	.16	.22	.16	.24	.13	.29	.18	.34	.13	.07			.06	.04	.04		.07	.08	.03	.09	.10	.12	.10	.10	.15
	.18	.16	.14	.25	.15	.10	.17	.10	.14	.21	.19	.05	.08	.05	.06		.07	.05	.13		.08	.06	.08	.06	.09	.16	.10	.11		.18
	.04	.13	.15	.05	.13	.12	.24	.17	.23	.13	.27	.26	.39	.22	.14			.04	.05			.04	.03	.05	.07	.04	.04	.06	.09	.11
	.17	.22	.25	.22	.23	.15	.29	.19	.30	.23	.35	.24	.39	.20	.08			.04	.09			.04	.06	.04	.10	.08	.07	.14	.08	.10
C	.21	.22	.29	.26	.19	.11	.16	.11	.22	.19	.16	.10	.12	.16	.08		.05	.07	.14		.05	.08	.09	.08	.10	.15	.14	.15	.04	.24
	.21	.22	.26	.22	.19	.14	.19	.14	.23	.24	.21	.08	.14	.05	.05		.06	.09	.18		.07	.10	.11	.11	.08	.14	.13	.14	.05	.25
	.19	.17	.20	.20	.22	.17	.25	.17	.21	.26	.20	.15	.13	.14	.05		.05	.08	.16		.06	.09	.10	.10	.11	.17	.12	.13	.05	.19
	.12	.16	.19	.19	.11	.10	.08	.05	.10		.06	.04	.04					.10	.07			.11	.08	.06	.04	.05	.14	.07	.06	.18
	.22	.19	.22	.27	.28	.23	.23	.12	.23	.16	.17	.03	.19				.05	.07	.14		.05	.08	.10	.09	.14	.12	.15	.15	.04	.25
	.17	.16	.18	.21	.16	.12	.27	.19	.21	.22	.33	.17	.31	.16	.07				.04				.03		.06	.09	.06	.08		.11
D	.06	.04	.05	.07	.11	.05	.04	.06	.07		.03		.04					.05	.07			.06	.04	.06	.05	.06	.05	.11	.19	.05
	.05	.11	.09	.06	.10	.04	.04	.05	.10		.08	.04	.04	.05	.05			.04	.06	.07		.05	.15	.16	.20	.14	.13	.31	.37	.08
	.09	.05	.07					.08	.13	.08	.13	.12		.17	.09					.14			.10	.18	.23	.15	.13	.29	.36	.06
	.08	.05	.06						.08		.09	.06		.07	.23								.10	.31				.17	.31	
	.09	.11	.13		.08		.05		.17		.17		.05		.18		.22	.13		.42			.26	.36	.12	.15	.20	.43	.64	.13
	.15	.10	.18	.08	.13	.06	.10	.07	.16		.13	.17	.04	.14	.15		.18	.18	.09	.22		.07	.10	.23	.16	.07	.12	.35	.46	.11
	.15	.14	.17	.11	.14	.13	.11	.05	.25	.05	.15	.08	.03	.09	.10		.17	.17	.17	.13		.19	.39	.25	.35	.36	.46	.60	.45	.24
	.08	.05	.13	.09	.14	.07	.10	.07	.08		.10	.06	.05	.08	.17			.06	.10			.08	.10	.25	.06	.07	.06	.23	.42	.06
	.11	.15	.18	.06	.10	.14	.16	.05	.23		.22	.04	.11	.05	.17		.13	.14	.06			.21	.19	.39	.21	.15	.14	.32	.39	.13
	.14	.14	.17	.08	.12		.09		.15	.06	.15	.05	.04	.07	.21		.17	.11	.08			.13	.23	.50	.10	.19	.17	.38	.43	.05
	.18	.20	.22	.15	.14	.17	.21	.03	.31	.10	.26	.06	.14	.07	.07		.08	.16	.08			.18	.14	.18	.24	.17	.23	.35	.19	.19
	.18	.16	.14	.19	.16	.15	.17	.05	.24	.16	.14	104	.04	.05	.06			.05	.13			.11	.08	.06	.09	.16	.14	.11	.06	.18
		.06	.08		.09		.06		.05		.11	.07	.06	.10										.22	.13			.21	.44	
	.10	.10	.12	.10	.09		.17	.04	.19	.17	.18	.08	.20	.09	.05			.04	.05			.04	.07	.10		.04	.08	.06		.04
	.07	.14	.15	.11	.13	.06	.11	.03	.19	.13	.23	.06	.24	.03	.10		.07	.18	.04			.10	.11	.07	.09	.13	.15	.18	.07	.06
E		.50	.63	.73	.43	.27	.26	.21	.29	.29	.19		.10		.08			.06	.20			.08	.10	.25	.06	.14	.13	.18	.25	.12
			.83	.31	.41	.17	.33	.23	.47	.27	.23	.04	.21		.05			.04	.11	.06		.05	.11	.15	.08	.14	.13	.20	.25	.16
				.67	.50	.21	.48	.28	.46	.33	.26		.20					.05	.14			.06	.08	.19	.05	.11	.10	.19	.25	.14
					.62	.21	.28	.23	.22	.31	.13		.10					.07	.22			.08	.11	.09	.06	.15	.13	.10	.09	.13
						.53	.52	.24	.31	.38	.15		.17					.06	.17			.07	.14	.07	.05	.13	.11	.13	.14	.11
							.45	.29	.33	.35	.15		.17					.05	.08			.13	.04	.07	.14	.12	.05	.08	.07	.15
								.48	.58	.46	.34	.13	.43					.04	.06			.05	.07	.05	.08	.10	.09	.10	.11	.13
									.31	.44	.24	.11	.26	.07				.06	.08			.07	.05	.07	.05	.06	.06	.04	.07	.05
										.54	.39	.14	.48	.04	.08			.04	.09	.05		.08	.12	.08	.13	.16	.04	.21	.21	.32
											.39	.21	.26	.20	.04				.08				.05	.14		.06	.06	.08	.07	.05
												.36	.55	.13	.10				.03	.04		.03	.10	.10	.11	.09	.09	.20	.16	.08
													.46	.33	.12										.04	.05		.07	.06	
														.14	.05										.04			.06	.10	.04
															.54			.06							.05			.09	.08	
																		.06										.14	.17	
F																	.40	.18	.40		.67	.25						.12	.14	.08
																		.57	.38	.17	.67	.55	.28	.40	.25	.50	.28	.25		.13
																			.43	.08	.33	.59	.38	.44	.27	.33	.40	.42	.13	.10
																					.67	.54	.33	.40	.25	.50	.42	.30	.20	.27
																							.19		.21	.20	.25	.17	.38	.08
G																						.44	.13	.25	.14	.20		.11		.08
																							.57	.46	.42	.53	.58	.35	.15	.17
																								.50	.69	.63	.66	.43	.25	.24
																									.44	.57	.38	.45	.33	.12
																										.70	.64	.50	.22	.30
																											.78	.58	.29	.31
																												.58	.31	.33
																													.45	.30
																														.18
H																														



TEXT-FIG. 10. Dendrogram derived from cluster matrix (text-fig. 9). Subclusters I–VIII represent major Palaeocommunity groupings referred to in the text.

however, differentiation remains evident; for example, *Sowerbyella* occurs in only three of the fifty-nine Shelve samples listed by Williams (1974, tables 6 and 7) whereas *Dalmanella* occurs in twenty-six. In the face of this dilemma the *Dalmanella* and *Sowerbyella* palaeocommunities (*sensu* Williams *et al.* 1981) have been included in a single category (palaeocommunity I; text-fig. 10); however, this procedure is not meant to obscure the clear differences which have been described. In particular, the sporadic stratigraphical occurrence of *Sowerbyella* has been considered to be a possible result of adaptations allowing mobility in response to currents (Williams *et al.* 1981).

It is particularly instructive to note that the closest association (C) between pre-Caradoc and Caradoc faunas are the 'anachronistic' examples, where type Lower Llandeilo faunas show a moderate degree of association with those from the Shelve Spywood Grit; the succeeding Upper Llandeilo faunas show even greater association ($C = 0{\cdot}44$) with Aldress Shale faunas. These faunas (D_{11} and D_{13} of Table 5) are closely related to *Nicolella*- and *Onniella*-dominated faunas from North Wales (Lockley 1980*a*; and Pickerill and Brenchley 1979) and confirm the observation of Wilcox and Lockley (1981) that Lower Llandeilo faunas represent 'an early expression of the type of association referred to as the *Bicuspina* set' (now the *Nicolella* palaeocommunity).

Relationships between diverse pre-Caradoc and Caradoc faunas are of obvious interest from an evolutionary viewpoint; Lockley and Williams (1981, p. 3) have already observed that there is an 'intriguing' relationship between diverse Llanvirn and Caradoc faunas and 'intercalated restricted faunas of the Llandeilo series'. Present data (text-fig. 8) suggest that over a period of about thirty million years (Ross *et al.* 1978) an equal number of associations (excluding obvious synonyms) were established, replaced, and re-established in the Welsh Basin area. Although this implies an average duration of about 1 m.y. for associations, in most cases they represent longer-lived palaeocommunities.

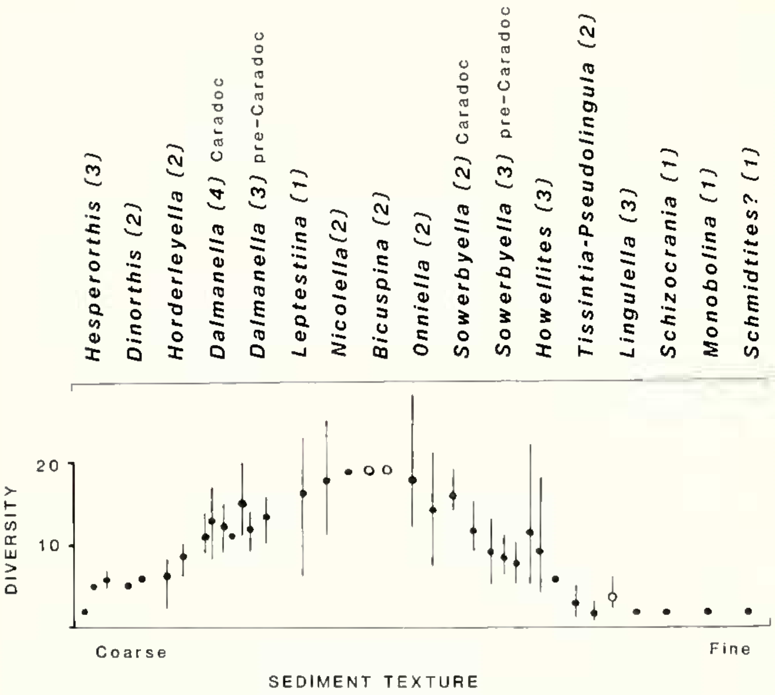
Clearly, Lower and Upper Llandeilo faunas do show significant relationships to descendant associations from Shelve. The 'mixed *Dalmanella*' palaeocommunity (I) was widespread and successful in mid-Wales in pre-Caradoc time. Despite being replaced locally during the latter part of the Llandeilo by *Tissintia–Pseudolingula*-dominated faunas (Wilcox and Lockley 1981, fig. 7), it survived successfully into Upper Llandeilo times in the Berwyn Hills area, where the fauna, described by MacGregor (1961), shows a high degree of similarity ($C = 0{\cdot}58$) to type Lower Llandeilo antecedents. Such faunas gave rise to equally diverse Caradoc associations (text-figs. 11, 12).

Palaeoecological perspectives

Although faunas from arenaceous Llanvirn and Caradoc facies exhibit some general taxonomic similarities (text-fig. 7) these are not as great as those exhibited by faunas associated with medium- to fine-grained facies. This suggests that such facies represented optimum environments for sustaining successful, long-lived stocks.

The physical stresses encountered in shoreface environments apparently restricted diversity, as in the *Hesperorthis* association, whereas in more open shelf regions there was more scope for the development of diverse, biologically accommodated faunas (cf. Sanders 1968, 1969). Finer-grained facies also exhibit reduced diversity, apparently due to other limiting physical stresses. Representative data from sources listed here (Table 1) allow a diversity plot complementary to text-figs. 6 and 7; this shows a clear trend towards maximum values in the middle part of the facies spectrum (text-fig. 11). The apparent relationships between the older 'mixed *Dalmanella*' palaeocommunity (I), and the *Nicolella* palaeocommunity (VIII) are emphasized by these observations, which show a theme of maximum diversity in related associations at different times.

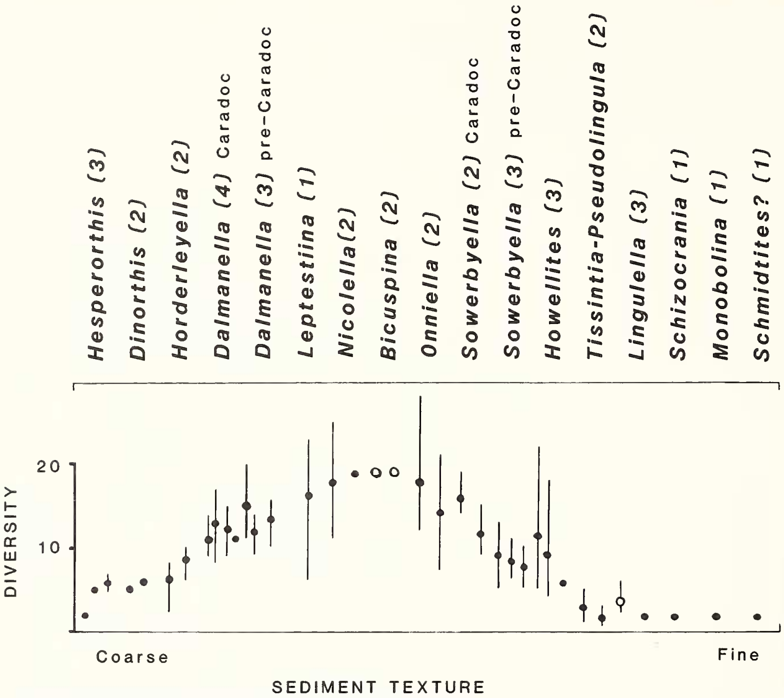
Since diverse *Dalmanella*-dominated faunas are locally associated with the *Nicolella* palaeocommunity in North Wales (see above) there is clearly some Llanvirn-to-Caradoc continuity, particularly in Welsh basin localities. The fact that the *Nicolella* palaeocommunity in the type Caradoc is poorly represented or found only in more offshore facies, *and* that type Caradoc *Dalmanella*-dominated faunas show no significant relationships with ancestral associations, serves to emphasize the importance of Welsh basin rather than basin-margin localities as the more stable sites for the



TEXT-FIG. 11. Plot of average diversity values from named associations and palaeocommunities arranged along a textural facies gradient; ranges given by vertical bars where known. Open circles refer to brachiopod diversities only and are therefore relative underestimates.

evolution of diverse, well-established palaeocommunities. Such observations do not support claims by Bretsky and Lorenz (1970, p. 2449) that 'diversity is negatively correlated with biotic stability'; their model is also disputed elsewhere. In contrast, described faunas from shoreface environments in Shropshire differ more radically. The more persistent physical environmental influences apparently led to more localized, rapid, and unpredictable changes in forms like *Dalmanella* and in the faunal composition generally.

Assuming that such a stability-stress model is valid it *may* be reasonable to consider the diverse, biologically accommodated communities as somewhat analogous to climax communities (Williams 1976). Hurst (1979*b*) has alluded to various problems associated with the 'climax community' model, suggesting that for any palaeocommunity successional stages must be clearly identified before conclusions are drawn. He also suggests that where perturbating influences interfere with stability it will be hard to identify such stages. These conclusions seem valid, support my observations as outlined above, and imply that a test of the climax model would be best undertaken



TEXT-FIG. 11. Plot of average diversity values from named associations and palaeocommunities arranged along a textural facies gradient; ranges given by vertical bars where known. Open circles refer to brachiopod diversities only and are therefore relative underestimates.

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Such palaeoecological considerations take into account the widespread Caradoc radiation of dalmanellids, which is a complex phenomenon best understood through the type of thorough analysis attempted by Williams (1963) and Hurst (1978*a*, *b*). They also indicate that well-established *Dalmanella*-dominated faunas are generally confined to more arenaceous near-shore facies and are replaced in finer-grained facies by *Howellites*, and *Onniella*-dominated associations (Hurst 1978*a*, fig. 5; Pickerill and Brenchley 1979, fig. 7). These latter associations are often more diverse than those containing *Dalmanella* (Hurst 1979*b*) although *Howellites* may occur in low diversity, sandy facies with *Heterorthis* and *Dinorthis*.

This radiation altered the established pre-Caradoc pattern. In many areas *Howellites* and *Onniella*, both fairly generalized forms, replaced *Dalmanella*, which developed some quite distinctive specializations such as the 'very coarse plicae' (Hurst 1979*a*, p. 246) of *D. unguis*. Paedomorphosis may have played an important role in such radical evolutionary developments (cf. McNamara, in press). Similarly allopatric speciation may have operated in restricted shoreface environments where environmental controls predictably reduced diversity more than in open-shelf environments, where stabilizing selection operated more effectively.

Although such trends had a limited effect on *Dalmanella*-dominated faunas they are more clearly seen (text-fig. 11) in older *Hesperorthis* and *Horderlyella* associations (text-fig. 11) and the Caradoc *Dinorthis* community (*sensu* Pickerill and Brenchley 1979).

CONCLUSIONS

In the final analysis few of the associations, communities, palaeocommunities, or sets named by the authors listed herein (Table 1) are so ill-conceived as to be considered invalid. There are a number of obvious partial synonyms such as the *Howellites* community (Pickerill and Brenchley 1979) and the *Howellites–Paracraniops* association (Lockley 1980*a*), or the *Onniella–Sericoidea* associations of Hurst (1979*b*) and Lockley (1980*a*); however, although some of these show very highly significant correlations ($C > 0{\cdot}68$) and can be grouped together in the fashion proposed above (text-fig. 10), others, as in the latter example, at best exhibit barely significant ($C = 0{\cdot}20$) coefficients of association and must therefore be considered separately.

In other cases, e.g. the *Pseudolingula* and *Bicuspina* sets and the *Dinorthis* community, constituent assemblages are so varied that they defy convenient classification.

Although faunas have already been assigned to various named associations (or communities, sets, etc.), eight (I–VIII) major groupings are identifiable (text-fig. 10). These are all represented by subclusters showing high or very high C values and reflect geographical proximity, age, and distinct facies preferences. Using the introductory rationalizations presented above they are best referred to as palaeocommunities and are in approximate order of age (oldest–youngest) as follows:

I. The 'mixed' *Dalmanella* palaeocommunity; age, Llanvirn to Llandeilo; distribution, the Llandeilo, Builth, Shelve, and Berwyn Hills areas; facies, typically fine, often calcareous clastics, mainly siltstones; includes the separately defined *Dalmanella* and *Sowerbyella* palaeocommunities and a part of the *Horderleyella* palaeocommunity (*sensu* Williams *et al.* 1981); ($\bar{C} = 0{\cdot}65$, range $0{\cdot}58$–$0{\cdot}78$).

II. The *Hesperorthis* palaeocommunity; age, Upper Llanvirn; distribution, Builth and Llandeilo areas; facies, typically coarse and granule–pebble sandstones; comment, this low-diversity palaeocommunity is distinct from the *Horderleyella* palaeocommunity (*sensu* Williams *et al.* 1981) although some intergrading occurs ($\bar{C} = 0{\cdot}67$).

III. The *Lingulella* palaeocommunity; age, late Upper Llanvirn to early Caradoc (Harnagian); distribution, Shelve area; facies, typically dark shales and mudstones (*sensu* Whittard 1979) and siltstones (Williams 1976); comment, includes four of the five assemblages used to define the *Lingulella* set (Williams 1976); the fifth (D_7) is more closely related to contemporary *Dalmanella*-dominated faunas from mid-Wales ($\bar{C} = 0{\cdot}68$, range $0{\cdot}61$–$0{\cdot}78$).

IV. The *Onniella* palaeocommunity; age Caradoc (latest Marshbrookian to Onnian); distribution, Shropshire type area; facies, typically bioturbated, often calcareous silts and muds, *sensu* Hurst (1979*b*); comment, consists of a pre-Onnian and an Onnian phase (respectively IVa and IVb of text-fig. 10); the former phase intergrades with the *Dalmanella* palaeocommunity; pooled C values for associations E_4–E_{12} average 0·52, range 0·46–0·58.

V. The *Dalmanella* palaeocommunity; age Caradoc (Marshbrookian); distribution, Shropshire type area; facies, typically sands and silts *sensu* Hurst (1979*b*), includes *Dalmanella*-dominated associations defined by Hurst (1979*b*); comment, intergrades, particularly through *D. unguis* association (Phase 3), with *Onniella* palaeocommunity (C values given above).

VI. The *Bancroftina–Kjaerina* palaeocommunity; age Caradoc (Longvillian–Woolstonian); distribution Shropshire (type area); facies, typically sands and silts *sensu* Hurst (1979*b*); includes associations defined by Hurst (1979*b*, *c*), see Table 4 ($\bar{C} = 0{\cdot}74$, range 0·67–0·83); comment, most highly correlated subcluster in type Caradoc.

VII. The *Howellites* palaeocommunity; age Lower Caradoc; distribution, Bala, Berwyn Hills, Breidden Hills, and Snowdonia; facies, typically mixed clastics mainly in the silt–fine-sand spectrum; includes Soudleyan faunas from all four areas which are in many cases dominated by *Heterorthis*, *Macrocoelia* (*Dinorthis* community of Pickerill and Brenchley 1979); also includes Lower Longvillian *Dalmanella* from Berwyns, which intergrades with palaeocommunity VIII ($\bar{C} = 0{\cdot}78$, range 0·74–0·84); comment, most highly correlated cluster.

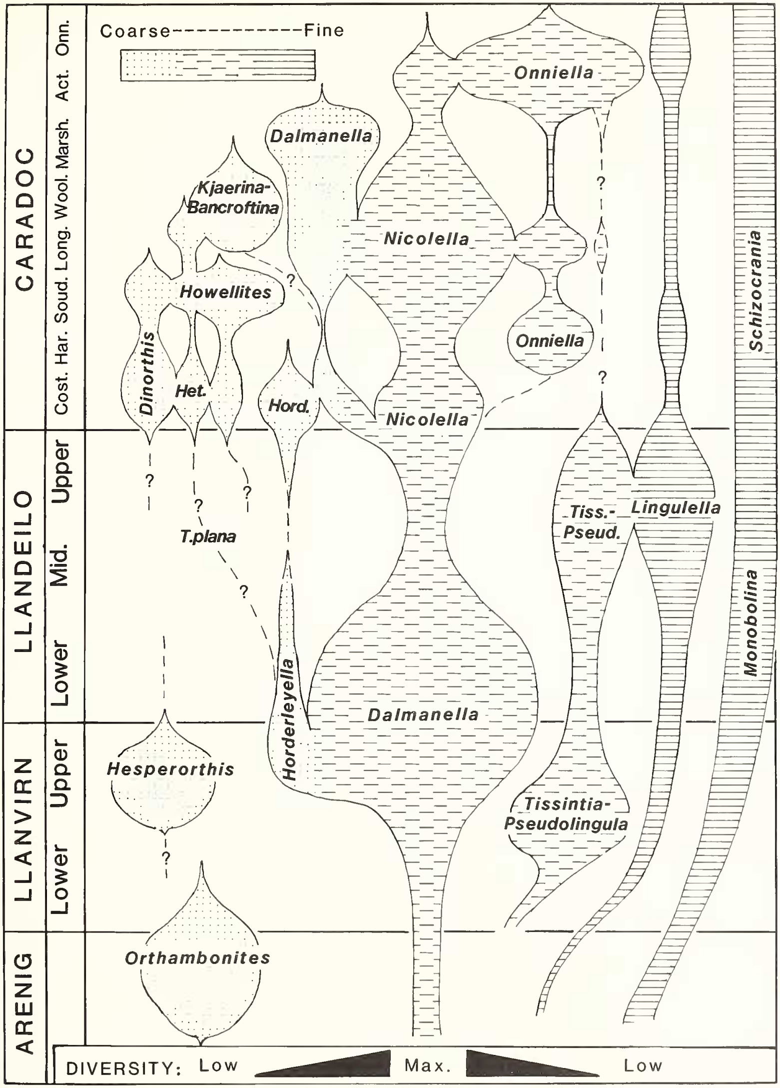
VIII. The *Nicolella* palaeocommunity; age Lower Caradoc; distribution, Bala, Berwyn Hills, and Shelve areas; facies, typically fine calcareous clastics and limestones; includes the Longvillian faunas of the former two areas and most of the Shelve *Bicuspina* set; ($\bar{C}$ value 0·59, range 0·44–0·72); comment, includes *Dalmanella*-dominated assemblages in the Bala and Shelve areas.

All identified palaeocommunities exhibit high to very high mean C values and largely reflect previous ideas on grouping of assemblages into higher categories. Sparse faunas such as those from Shelve and assemblages representative of the *Tissintia–Pseudolingula* association do not show high correlations. The same is true for a few other faunas which, in addition to being taxonomically distinct, are geographically isolated. The inferred evolutionary relationships between the main palaeocommunities and other associations outlined above are presented in text-fig. 12, which also incorporates generalized facies and diversity gradients. It is particularly important to note that the diverse, ancestral 'mixed *Dalmanella*' palaeocommunity gave rise to the *Nicolella* palaeocommunity and that descendant *Dalmanella*-dominated faunas, epitomized by the Shropshire palaeocommunity (V), show significantly changed taxonomic composition and facies preference. The relationship of the *Nicolella* and *Onniella* palaeocommunities is first evident in the early Caradoc and is noted again in mid and later Caradoc times.

Faunas dominated by *Heterorthis* and *Dinorthis* appear in the early Caradoc of Shropshire where the term *Dinorthis* community (*sensu* Pickerill and Brenchley 1979) is locally appropriate. Contemporary faunas from Dyfed (text-fig. 5) are dominated by *Heterorthis* and *Howellites*, both of which, as depicted in text-fig. 12, remain dominant in the *Howellites* palaeocommunity, whilst *Dinorthis* plays a subordinate, intergrading role. *Heterorthis* probably arose from ancestral *Tissintia* (Havlíček 1970), which is represented in Wales by three distinct species (Lockley and Williams 1981). The most likely ancestor is *T. plana*, a large species associated with sandy facies in Dyfed. It is more specialized than *T. immatura*, which persists in more argillaceous type Llandeilo facies (Wilcox and Lockley 1981) and may be the ancestor of some closely related Caradoc dalmanellids.

Considerations of evolutionary relationships between low diversity, inarticulate-dominated faunas of the argillaceous facies indicates limited change through time; only *Monobolina* exhibits apparent species level evolution (Lockley and Williams 1981). *Schizocrania* occurs with *Monobolina* in many assemblages but can quite reasonably be considered representative of a different palaeocommunity (*sensu* Williams *et al.* 1981) because of its very different life habits (Lockley and Antia 1980). Locally both forms are associated with the *Lingulella* palaeocommunity.

Finally, the diversity-stress model presented here is evidently supported by analogous examples



TEXT-FIG. 12. Inferred evolutionary relationships between named associations and palaeocommunities from the Ordovician of Wales and the Welsh Borderland. (See text for details.)

elsewhere. Silurian models in particular have been the subject of much debate, not least because of speculations about absolute depth (Hancock, Hurst and Fursich 1974; Johnson and Potter 1976; Shabica and Boucot 1976). Although this aspect of the debate need not concern us here, it is evident that some models are broadly analogous, showing that 'diversity . . . increases with depth', and eventual decreases in the deepest facies (Hancock *et al.* 1974). More recently, Hurst and Watkins (1981) have emphasized such analogous patterns by noting that 'Caradoc and Ludlow species diversity increases into more distal shelf environments' but then, in certain cases 'decreases in offshore environments'. Such near-to-offshore diversity trends have also been recorded for modern brachiopod faunas (Foster 1974).

Since recurrent diversity profile patterns would hardly . . . 'develop in stratigraphically separated sequences if' they 'did not reflect original patterns' (Hurst and Watkins 1981) the model receives further support. However, it should be stressed that the model is only tentative and assumes that the facies gradients can be equated with an onshore–offshore palaeoenvironmental transect. More convincing interpretation of a greater variety of sedimentary facies is needed to infer palaeocommunity habitats confidently. When this is achieved the potential for inter-community comparisons will be realized more fully.

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